Stunkard.

# Studies On North American Polystomidae Aspidogastridae And Paramphistomidae

# STUDIES ON NORTH AMERICAN POLYSTOMIDAE, ASPIDOGASTRIDAE AND PARAMPHISTOMIDAE

BY

HORACE WESLEY STUNKARD

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I HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER MY SUPERVISION BY HORACE WESLEY STUNKARD

ENTITLED STUDIES ON NORTH AMERICAN POLYSTOMIDAE, ASPIDOGASTRIDAE AND PARAMPHISTOMIDAE.

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Henry B. Ward
In Charge of Thesis

Henry B. Ward
Head of Department

Recommendation concurred in:*

J. S. Kingsley
F. Smith
V. E. Shelford
J. A. Sperry

Committee on Final Examination*

*Required for doctor's degree but not for master's.

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## I. Introduction

The knowledge of the trematodes of North America is very scanty. Information regarding the group in this country is almost entirely confined to scattered papers describing new species, and many are so brief that they are of little value. A comparatively small number of investigators have worked in this field, and practically all our knowledge is the result of the last fifty years. As a consequence the trematode fauna of North America remains largely unknown. Complete knowledge and a final classification will be possible only when the structure of all the various forms is worked out and their complicated life histories are solved. Comprehensive studies on the morphology of the larger groups have been impossible because so few forms were known. It is apparent that the solution of life history problems, involving the discovery of the developmental cycle and the establishment of the identity of the cercaria and adult into which it develops, is largely dependent on advance knowledge concerning the structure and classification of the adult forms. The verification of life histories requires experimental proof, for as has been pointed out repeatedly, larval adaptations of cercaria and the absence of so many adult characters make the establishment of specific identity between cercaria and adults by means of structural comparisons very difficult and unsafe.

In Europe, by virtue of a longer as well as a more extensive and intensive study, many more species are known,

the structure and classification of the forms have received considerable attention, and a few complete developmental cycles are known.

In the first classification of the group, Zeder (1800) separated three genera Monostoma, Distoma, and Polystoma on the basis of the number of suckers. Burmeister (1856), also basing ~~basing~~ his classification on the character of the adhesive apparatus, suggested a division into (1) Malacobothrii for the distomes, (2) Pectobothrii for the polystomes and (3) Aspidobothrii for Aspidogaster. In the same year Leuckart added the factors of habitat and type of development to the taxonomic characters and proposed two families, (1) Distomea for endoparasitic forms which develop with a metamorphosis, and (2) Polystomea for ectoparasitic forms which have a direct development. Van Beneden's (1858) classification into Monogenea and Digenea was based entirely on the manner of development. Monticelli (1892) considered structural features of paramount importance in taxonomy and proposed a classification on the nature of the adhesive organs. He considered the Trematoda as an order and divided it into three suborders, Heterocotylea, Aspidocotylea and Malacocotylea, thus establishing again the classification of Burmeister.

Many writers, Braun (1893), Looss (1899), Pratt (1900), accept the idea of Monticelli, while others, Lühe (1909), and Odhner (1912) follow the classification of van Beneden. Pratt (1900) speaking of the Monogenea and Digenea of van Beneden says, " The great additions, however, which have been

made in recent years to our knowledge of the trematodes have rendered it increasingly difficult to use these distinctions satisfactorily". Gamble (1910) altho following the system of van Beneden says, "The classification of the trematodes according to their life histories breaks down completely in the case of certain forms. Thus the life history of Gyrodactylus is probably digenetic rather than monogenetic". He cites the monogenetic development of Aspidogaster and the metastatic development of the Holostomidae as additional instances of the inadequacy of the system. Further evidence against the arrangement is found in case of the Aspidogastridae, as this family contains genera in which the development is monogenetic and stichocotyle which has an intermediate host. Since the life history is so complex, is so little known and in so many instances fails to effect a natural division of the group, it can not be retained as the fundamental basis of classification. In other groups of the animal kingdom, taxonomy is founded on both anatomy and embryology and a natural classification of the trematodes must be based on a consideration of both structure and development. Information concerning the life history is very scanty and the type of development as well as the primitive structural features have been greatly modified as the result of parasitism, but as these coenogenetic changes are discovered, the fundamental morphological agreement and true relationships of the forms will be established.

This paper contains results of a study on the

structure and classification of North American representatives of the families Polystomidae, Aspidogastridae and Paramphistomidae. These three families because of certain structural and developmental features are of particular interest and importance not only in the taxonomy but also in the phylogeny of the trematodes. The Polystomidae differ from all other known Heterocotylea in that its members are endoparasitic; the Aspidogastridae are both ecto and endoparasitic, both monogenetic and metastatic, and in the adult condition are parasites of both vertebrates and molluscs; while the Paramphistomidae are the only forms retaining a primitive posterior sucker. These facts are significant and it is probable that further study into the structure and life history of these forms will throw considerable light on the general problems of development and taxonomy of the trematodes.

During the past three years the writer has made parasitological examinations of over three hundred North American fresh water turtles. These comprise sixteen species collected from widely scattered localities. For assistance in securing this material grateful acknowledgments are due Dr. N. A. Cobb of Washington, D. C., Professor A. W. Orcutt of Denison University, Professor W. E. Burge of the University of Illinois, Professor J. E. Ackert of Kansas State Agricultural College, and Professor W. W. Cort of Macaelester College. The material of Alassostoma parvum was collected and turned over to me by Mr. T. B. Magath. A type specimen of Polystoma coronatum Leidy from the U. S. National Museum was placed at

my disposal for study. The work was begun at the suggestion of Professor Henry B. Ward and carried on under his direction. A large part of the material used in the investigation, both new species and identified material for comparative study, came from his extensive private collection, and for this material as well as for criticisms and suggestions in the course of the work the writer wishes to express his sincere appreciation.

## II. Methods of Technique

All the forms described in this paper were studied as toto mounts, where sufficient material was available sections were made, and many of the parasites collected by the writer were studied alive. For the study of the living worm, the specimen was placed on a slide in a drop of water or normal saline solution and examined with the low powers of the microscope. In the smaller worms the water supported the cover glass sufficiently to permit the animal to move freely. As the water evaporated and the worm became flattened the ducts of the excretory system appeared as dark lines. The importance of the live study can not be overemphasized as it is the best method of tracing the excretory system and a careful observation of the animal as it moves gives a more accurate and complete knowledge than can be obtained from a study of fixed material alone. By observing the living animal as it moves it is possible to measure the extent of normal variation that occurs in a single specimen as different

shapes are assumed concomitant with the movements of the animal, while in forms with such soft bodies and variable shapes a study of preserved material alone is apt to give a perverted idea concerning true morphological relationships of organs and systems. Stupification by the use of chloretone and magnesium sulfate was tried on the larger worms but with indifferent results. The shaking method of Looss gave well extended specimens and if the killing fluid is used warm it aids in relaxing and expanding the worm as it is killed. No ill effects were noted in the tissue as a result of the use of warm killing fluids. Gilson's, vom Rath's, Tellyesniczky's and Kleinenberg's fluids all gave good fixation, as did a saturated aqueous or 70% alcoholic solution of corrosive sublimate to which from 3 to 5% of glacial acetic acid had been added. The material was preserved 75 to 80% alcohol.

For the anatomical study both toto preparations and serial sections were used and each supplemented the other. Sections for general morphological study were cut 10 to 15 micra in thickness, and those for histological purposes 5 to 8 micra. When sufficient material was available, sections were cut in transverse, frontal and sagittal planes. To secure more transparency some of the worms to be used as toto preparations were flattened between slides, while others were maintained in their normal proportions by supporting the cover glass. Such a support is especially necessary to prevent the cover glass from flattening and distorting the normal shape of the apidobothrids and to avoid crushing the caudal disc of

the polystomes.

For the staining of specimens to be mounted in toto, uniformly successful results followed the use of carmine stains. Overstaining, with subsequent rapid destaining of the parenchyma in 70% alcohol to which 2 to 3% of HCl had been added leaves the internal structures stained and sharply defined. Better results were obtained by using the stain diluted two or three times with the proper diluent and allowing a longer time for penetration. Some excellent toto preparations were secured by the use of haematoxylin stains, but in general, better and more consistent results were obtained by the use of carmine stains. La Rue (1914) says, "It is noteworthy that the carmine stains give beautiful preparations of trematodes in toto, but fail almost completely for cestodes." Mayer's paracarmine, carm alum and alcoholic cochineal, Guyer's alum cochineal, and Grenacher's borax carmine all gave splendid toto preparations. The alcoholic stains have the advantage that they penetrate more rapidly.

For the staining of sections the writer found the carmine stains practically worthless. Delafield's, Ehrlich's acid, Mayer's haemalum and Heidenhain's iron haematoxylin all gave excellent results in the staining of sections, and are equally valuable for staining material before sectioning. Ehrlich's acid haematoxylin unless diluted with distilled water formed a flocculent precipitate that made it unsuitable for staining sections on the slide. The method most used and the one that gave the best results was to stain in toto in

Ehrlich's acid haematoxylin, and then destain and counter stain the sections on the slide. One % HCl in 70% alcohol was used to destain and erythrosin dissolved in 85% alcohol for a counter stain. This method has the advantages that it is (1) extremely rapid; (2) toto staining renders the material easy to manipulate and facilitates orientation in embedding; (3) destaining and counterstaining in the higher grades of alcohol not only saves time but eliminates the danger of the sections coming off the slide, which sometimes occurs in the weaker alcohols or water. This method uniformly gave good results, sharply differentiating the nuclear and cytoplasmic elements. For cytological work, Heidenhain's iron haematoxylin was used almost entirely, both singly and counterstained with Orange G, erythrosin or picro-fuchsin.

## III. Polystomidae

In 1758 Roesel von Rosenhof described and figured a leech, "Egel", from the urinary bladder of the frog. Diesing (1850) and Braun (1890) refer to the form as Polystoma integerrimum, the well known parasite of the urinary bladder of the frog, described by Frölich (1791) as Linguatula integerrima. M. Braun (1792) described Planaria uncinulata from the urinary bladder of the green water frog and his description is so specific that there can be no doubt that he had the same form described by Frölich the previous year. In the original genus Polystoma Zeder (1800) included P. serratum Fröhlich, the type of Linguatula Fröhlich 1789; P. pinguicola Treutler, a very doubtful form described by Treutler in 1793 from a fatty swelling near the ovary of a woman, and designated as the type of a new genus Hexathyridium; and Linguatula integerrima Fröhlich which he rechristened Polystoma ranae. In his description of the genus he states, "Vorderende mit mehreren Saugwartzen" altho Braun (1792) had described the correct orientation of the worm with the suckers and hooks at the posterior end.

Rudolphi (1809) regarding Polystoma Zeder says P. integerrimum is a true species, the species reported by Treutler is uncertain and the rest are pentastomes. P. J. van Beneden (1849) discovered the embryo of the Linguatulida and located them with the arthropods. Braun (1890) and Looss (1902) advocate the suppression of the genus Hexathyridium. This would leave P. integerrimum as the only

original species remaining in the genus.

Polystoma ocellatum, the second species of the genus, was described by Rudolphi (1819) from the throat of Emys europa. Kuhl and Hasselt (1822) described the same form as P. mydae from the nose of Halichelys atra. Blainville (1828) created a new genus Hexacotyle to contain P. thynii Delaroche, P. integerrimum Fröhlich and P. ocellatum Rud., and named H. thynii as type. Diesing (1850) restored the genus Polystoma and included the two species P. integerrimum and P. ocellatum. Several pentastomes and ectoparasitic trematodes have been ascribed to the genus and later removed to other genera. P. appendiculatum Kuhn 1829 was designated by Diesing (1850) as type of a new genus Onchocotyle, and P. armatum Dujardin 1845 had previously been described by Leuckart as the type of a new genus Diclybothrium.

The trematodes with several posterior suckers were included in the tribe Polycotylea by Diesing. Taschenberg (1879) proposed a division of this group into two families, Tristomea and Polystomea, the latter to contain the four subfamilies, Octobothriidae, Polystomidae, Microcotylidae and Gyrodactylidae. In the subfamily Polystomidae he included the genera Polystoma, Onchocotyle, Erpocotyle and Diplobothrium; and in the genus Polystoma the species P. integerrimum and P. ocellatum. St. Remy (1891) followed the arrangement of Taschenberg. Monticelli (1892) proposed the suborder Heterocotylea with five families, and in the family Polystomidae included the subfamilies Polystominae,

Octocotylinae and Microcotylinae. His subfamily Polystominae is identical with Taschenberg's subfamily Polystomidae except that he added the genus Sphyranura. He raised Gyrodactylidae to equal rank with the Polystomidae but considered Octocotylinae as a subfamily of the Polystomidae altho van Beneden and Hesse (1863) had ranked the Octocotylidae as a family. Braun (1893) followed the classification of Monticelli. Pratt (1900) followed the same classification with certain modifications that had been proposed by Braun, Cerfontaine, Goto, St. Remy and others. He retained the three subfamilies Polystominae, Octocotylinae and Microcotylinae. Benham (1901) raised the Microcotylidae to family rank and in the family Polystomidae included the subfamilies Polystominae and Octocotylinae. In all the classifications discussed above, the family Polystomidae had no clearly defined limits, and it appears as tho the authors had grouped together forms with certain superficial similarities and then formed a family diagnosis to include them. The genera showed wide differences in the number and character of suckers, as well as in the type of digestive and reproductive organs.

From all this confusion Monticelli (1903) constructed a new classification of the Heterocotylea. He separated the forms on the basis of adhesive apparatus and proposed a new arrangement of the group. In this classification there are twelve families arranged in two tribes: Olyocotylea, containing the families Tristomidae, Monocotylidae, Udonellidae, Calceostomidae, Gyrodactylidae and Dicotylidae; and Polycotylea

containing the families Polystomidae, Octocotylidae, Hexacotylidae, Platycotylidae, Pleurocotylidae and Microcotylidae. The family Polystomidae contained the single genus Polystoma, and the species P. integerrimum, P. ocellatum, P. oblongum, P. coronatum and P. hassali.

Odhner (1912) discussed the relationships of the ducts of the female genital system in various trematode and cestode forms. He is convinced that as was pointed out by Stieda (1871), Laurer's canal of the trematodes is homologous with the vagina of the cestodes. Looss (1893), Goto (1894) and several other writers consider Laurer's canal of the Malacocotylea as homologous with the genito-intestinal canal of certain Heterocotylea, and not as homologous with the vagina of the cestodes. Odhner argues thar Laurer's canal is the primitive vagina of the trematodes, and that there has been a change of vaginal function from this canal to the terminal part of the uterus, with the resulting degeneration of the former duct. It now serves he says only to carry off excess spermatozoa, together with yolk and shell substance not used in the formation of the eggs. He adds,"Auf die Frage, warum die Vaginalfunktion ihrer Sitz gewechselt hat, lässt sich endlich keine bestimmte Antwort geben; es ist nur als eine Tatsache hinzunehmen."

Odhner argues that in the group of the monogenetic trematodes, two very different morphological structures are included under the term vagina. One present in the Tristomidae, Monocotylidae and Gyrodactylidae opens to the exterior on the left side of the ventral surface, and at the inner end is

enlarged to form the seminal receptacle. This tube he considers homologous to the vagina of the cestodes and the Laurer's canal of the digenetic trematodes. The other structures which he considers as not homologous to this true vagina are the ducts of the Octocotylidae, Polystomidae, and Microcotylidae, which function as vaginae and open into the vitelline collecting ducts. These are more or less paired and open to the surface either ventrally, laterally or dorsally. For these he proposed the name "Ductus vaginales". Considering the question of whether the paired or unpaired condition of these ducts is primitive, he argues that originally the duct was unpaired and opened ventrally, that the opening became divided and the duct split, "so haben wir zunächst in dem Y-förmigen Ductus von Rajonchocotyle ein Stadium der sich entwickelnden paarigen Trennung der Gänge zu erblicken". A further lateral migration would give the lateral openings of Polystoma, and in certain forms the openings have migrated dorsally and fused giving a single dorsal tube. He says the genito-intestinal canal is not homologous with Laurer's canal and since he can find no for it concludes that it has arisen sui generis.

He says, "die verschiedene Ausbildung der jetzt besprochenen Genital_wege von grundlegender Bedeutung für das natürliche Monogenensystem ist". On the basis of these differences in the female genital ducts he divides the "Monogenea" into two suborders; Monopisthocotylea in which the genito-intestinal canal is absent and which have a "true vagina", and Polyopisthocotylea in which the genito-intestinal canal

is present and which has the so called "Ductus vaginales". In the first group he included the families Tristomidae, Monocotylidae, Udonellidae and Gyrodactylidae; and in the second the families Polystomidae, Microcotylidae and Octocotylidae.

Discussing the classification of Monticelli (1903), he considers the number of suckers of secondary importance, and the classification lacking in important systematic significance. He points out however that by the removal of the genus Sphyranura from the Olyocotylea, the first of Monticelli's two tribes, it agrees entirely with his suborder Monopisthocotylea. In the second of Monticelli's tribes, he says the Diclidophorinae and the genus Hexacotyle should be removed from the family Octocotylidae and placed with the Microcotylidae, since they more nearly agree with the latter forms in internal structure.

The next year Odhner (1913) reaffirms his idea of the homology of the vagina of the cestodes and the Laurer's canal of the distomes, but states that his denial of the homology of the genito-intestinal canal and Laurer's canal had been based on an incorrect description by Cerfontaine when he described an unpaired vagina as present in the genus Dactylocotyle. Odhner reinvestigated this point and found the error, and in view of his discovery he concludes that the "true vagina" of the Monopisthocotylea which he had homologized with the Laurer's canal of the distomes is never present together with the genito-intestinal canal. From this he

decided that the "true vagina" of the Monopisthocotylea is homologous with the genito-intestinal canal, and homologizes the enlargement at the inner end of the genito-intestinal canal of Hexacotyle with the seminal receptacle of the Monopisthocotylea. In his statement that the genito-intestinal is homologous to Laurer's canal he agrees with Looss and Goto. Still maintaining the homology of the "true vagina" and the genito-intestinal canal he is at a loss to account for the paired vaginae and explains these as arising sui generis. Starting with a wrong assumption, viz., that Laurer's canal is homologous to the vagina of the cestodes, he has missed the truth in his entire discussion, and when at a loss to explain a structure, has derived it sui generis. The entire discussion shows that because of the retention of this incorrect assumption he has misinterpreted the true morphological relations.

Goto (1894:154-173) reviews the literature up to that date and gives a careful and detailed study of the homology of the canalis genito- intestinalis. He gives a very clear and comprehensive analysis of the question and summarizing evidence from a wide study of ectoparasitic forms, he concludes that the genito-intestinal canal and Laurer's canal are homologous and that neither are homologous with the vagina of the Monogenea. He shows that in the group there is a perfect series of vaginae from a truly paired to a truly unpaired condition. He discusses the idea of Braun who regarded the presence of a single vagina as the result of a simple atrophy of one of the originally paired vaginae, with the conclusion that the relations of the ducts "point strongly to the view

that the unpaired vagina has been formed by the union and subsequent displacement of the originally paired vaginae, and not as Braun supposes by the atrophy of one of them." If we dismiss the assumption that the vagina of the monogenetic trematodes is homologous to Laurer's canal, there is no evidence to support the idea that the single vagina is not homologous to the paired vaginae. In fact, Odhner describes the paired vaginae as arising from a single unpaired tube, probably ventral in position. He derives this tube sui generis, and cites no reason why it is not homologous with the ventral unpaired vagina of Monopisthocotylea. Further, he gives no means of distinguishing between the two.

In the course of the present study, the histological character and the relative position and relationships of the ducts of the female system submit evidence strongly supporting the contention that Laurer's canal is homologous with the genito-intestinal canal, and affords no evidence that these ducts have any further homologue. A careful review of the literature and the study of the ducts in the three families discussed in this paper, has convinced me that Laurer's canal is homologous to the genito-intestinal canal; and the vagina of the Monopisthocotylea is homologous with the originally single, subsequently paired and secondarily fused vaginae of the Polyopisthocotylea. It makes no difference whether we regard the single or paired condition as primitive. If we start with a single unpaired vagina as Odhner described for the Monopisthocotylea, by a division of the external part and

subsequent lateral migration of the openings the paired vaginae of the Polyopisthocotylea are explained. These ducts entering the body from the sides, lying parallel with the vitelline ducts and discharging into the same cavity, fused at their internal end with the vitelline ducts and this union continued outward to the location where the vitelline ducts turn toward the follicles and the vaginae branch off to open to the exterior. The advantage of a single duct over two ducts lying side by side is obvious, and the fusion of two parallel ducts is not uncommon in other groups. With a further dorsal migration of the openings of the vaginae there would be a separation of the vitelline and vaginal canals, and a dorsal fusion of the vaginae would give the single dorsal vagina of Octobothrium, Axine and Microcotyle. I agree with Odhner that the seminal receptacles of Sphyranura are homologous to the the paired vaginae of Polystoma, and that this furnishes a splendid example of the change of function whereby the terminal part of the uterus has assumed the copularory function. With further specialization in this direction due to the endoparasitic habit and self fertilization, the vaginæ of the distomes has disappeared entirely. It remains now only to account for the absence of the genito-intestinal canal in the Monopisthocotylea. Odhner states that this is homologous with the Laurer's canal, and in his (1912) paper called attention to the fact that Laurer's canal is a "ganz rudimentary organ" which serves no essential function in the body. The vestigeal character of Laurer's

canal is believed by most writers, Looss, Monticelli, Brandes, Goto, etc. It is entirely lacking in some distome groups, and in others is represented by a blind sac opening from the ootype. Haswell (1907) described in certain Australian polyclads a tube which formerly had been considered an accessory or dorsal vagina but which in certain forms opened into the intestine. The presence of this genito-intestinal canal in polyclads, he says, "strengthens the contention, so ably supported by Goto, that the genito-intestinal canal and not the vagina of the Heterocotylea is the equivalent of the Laurer's canal of the Malacocotylea. Mac Callum (1913) described a short muscular tube in Thoracocotyle croceus which arises from the ootype and runs anteriorly for a short distance and ending blindly. Since the genito-intestinal canal is homologous with Laurer's canal and the latter is known to be a vestigeal structure, it appears reasonable to suppose that it has degenerated in the Monopisthocotylea. There appears a possibliity that the Monopisthocotylea instead of having lost a genito-intestinal canal may have arisen from a group of the Turbellaria which had no homologous structure.

The absence of the genito-intestinal canal in the Monopisthocotylea is undoubtedly a feature of distinct taxonomic importance, and the work of Odhner is an advance step in the formation of a natural system and a final classification of the monogenetic forms. Since the arrangement of Monticelli, based on the character of the adhesive apparatus, so nearly agrees with that of Odhner which is based on the

presence or absence of a genito-intestinal canal, it appears that both these features are of large importance in the taxonomy of the group.

Odhner (1912) argues that the removal by Monticelli of Sphyranura from the family Polystomidae on the basis of the difference in number of suckers is not justified. As previously stated, the writer agrees with Odhner that the seminal receptacles of Sphyranura are homologous with the vaginae of Polystoma, and the agreement in type of genital ducts demonstrates a closer relationship between these genera than is assigned in the system of Monticelli. Sphyranura undoubtedly should be placed with the Polyopisthocotylea. There are, wide and fundamental differences between it and the genus Polystoma, and while future researches may discover intermediate forms which will make it possible to include them with certainty in a single family, for the present such a grouping is hardly justified, and the two families should be retained, altho the name Diclotylidae of Monticelli does not conform to the rules of zoological nomenclature.

The family Polystomidae as considered in this paper contains only the genus Polystoma. The members of this genus are widely distributed, species have been described from all the continents except South America. The species are not only widely distributed geographically, but also vary greatly in type of host and location within the host. They are parasitic in the urinary bladder of frogs and toads and on the gills of frog larvae, and also infest the urinary bladder and pharyngeal cavity of many species of turtles.

The structure and development of Polystoma integerrimum has been investigated by Stieda (1870), Zeller (1872) and (1876), Willemoes-Suhm (1872), Halkin (1902), Goldschmidt (1903), and André (1910). The descriptions of P. ocellatum by Rudolphi (1819) and Kuhl and Hasselt (1822) are very brief, that by Willemoes-Suhm contains one plate, and Looss (1885) figures the structures at the distal ends of the excretory tubules. The description of P. oblongum Wright (1879) contains sufficiently detailed information for a specific diagnosis and is illustrated by three figures. Stafford (1905) reported P. oblongum from the palate of Chrysemys picta and from the same location in Chelydra serpentina, but since Wright originally described the species from the urinary bladder of Aromochelys odoratus, Braun reviewing Stafford's article considered the form from the oral cavity as a different species. Leidy's (1888) description of P. coronatum is so brief that it is almost valueless, but a type specimen has been available for the present study as a mounted toto preparation and many additional points of structure are added to the original description. P. hassali was described by Goto (1899) from the urinary bladder of Cinosternum pennsylvanicum and has been collected by the writer from the urinary bladder of Aromochelys odoratus and Chelydra serpentina. Additional data corrects and supplements the description of Goto. The form described by Leidy as P. oblongum was reinvestigated by Goto (1899) and proved to be a different species from that described by Wright, but the material he reports was in such a poor

state of preservation that renewed study was impossible and so the form must remain unknown. Johnston (1912) described P. bulliense from the urinary bladder of two species of Hyla from New South Wales, Australia. Beauchamp (1913) described P. alluaudi from an unknown batrachian from the lower prairies of Kinangop, Africa; the material was collected by the African expedition of Alluaud and Jeannel. Stewart (1914) described P. kachugae from the urinary bladder of the water tortoise, Kachuga lineata, at Lucknow, India.

In the genus Polystoma, present evidence supports the validity of the following species.

P. integerrimum Fröhlich 1791. From the urinary bladder of frogs and toads and the gills of frog larvae, Europe.

P. ocellatum Rudolphi 1819. From the throat and nasal cavity of Emys europa and Halichelys atra, Europe.

P. oblongum Wright 1879. From the urinary bladder of Aromochelys odoratus, North America.

P. coronatum Leidy 1888. From the fauces of the terrapin, North America.

P. hassali Goto 1899. From the urinary bladder of Cinosternum pennsylvanicum, Aromochelys odoratus, A. carinatus and Chelydra serpentina, North America.

P. bulliense Johnston 1912. From the urinary bladder of Hyla phyllochros and H. leseurii, Australia.

P. alluaudi Beauchamp 1913. From an unknown batrachian, Africa.

P. kachugae Stewart 1914. From the urinary bladder of

Kachugae lineata, Asia.

P. orbiculare n. sp. From the urinary bladder of Pseudemys scripta and Chrysemys marginata, North America.

P. opacum n. sp. From the pharynx of Trionyx ferox and Malacoclemmys Leseurii, North America.

P. megacotyle n. sp. From the mouth of Chrysemys marginata, North America.

P. microcotyle n. sp. From the mouth of Chrysemys marginata, North America.

With the exception of P. integerrimum, the members of the genus are very rarely found and the number of individuals discovered is very small. Wright described P. oblongum from two specimens; Leidy, P. coronatum from four specimens; Johnston had sixteen specimens of P. bulliense; Beauchamp described P. alluaudi from a single specimen; Stewart had only two specimens of P. kachugae. The writer had only a limited number of specimens of any species; P. microcotyle was described from a single worm; P. orbiculare from nine specimens; P. opacum and P. megacotyle each from three specimens. Because of the very limited amount of material, it has been impossible to attempt special technique to differentiate the various organ systems, and the descriptions are therefore incomplete in certain particulars. The general morphological features are however described in sufficient detail that clear specific diagnoses may be made, and in certain instances the finer structure and histology of the organs has been described.

## Anatomy and Histology of the Polystomidae.

The species that have been included in the genus Polystoma show a much wider range of structural variation than is usually present in a natural genus. There are wide differences in the type of digestive and reproductive systems, and variation exists in the type of adhesive apparatus. Zeller (1876) described two forms of P. integerrimum, one which became mature in the urinary bladder of the frog, and the other which became mature on the gills of the frog tadpole. These two forms of the parasite show wide differences in size and internal structure. The form which becomes mature in the urinary bladder is much larger, has a lobed testis, external vaginae and a long coiled uterus which contains many eggs. The form maturing on the gills of the tadpole has a spherical testis, lacks external vaginae, and has a small uterine cavity in which a single egg develops. These results are so unusual that his work should be carefully repeated and confirmed. Halkin (1902) and Goldschmidt (1902) have investigated the early stages in this form but the writer has been unable to find any reference to work on the later larval stages. The condition described by Zeller is unparalleled in the group and one is led to strongly suspect that he confused two different species. If it is true that a difference in the physiological life history will make such a profound difference in the structure of the adult animal, it will be necessary to revise our ideas concerning morphology and taxonomy.

Shape and Size. All the worms included in this genus have a flattened, elongate oval body which at the posterior end turns ventral and is expanded into a large muscular disc or cotylophore. The body is more or less pointed at the anterior end and at the posterior end narrows suddenly just before enlarging to form the caudal disc. As in all trematodes the shape is subject to considerable variation as the animal elongates and contracts. Locomotion is accomplished by attaching the anterior sucker while the caudal disc is being moved, and as a result of the terminal attachments and the "looping" method of progression, the dorsal line of the body is more or less arched and the ventral surface is concave. There is wide variation in size; P. integerrimum, the largest known species measures up to 13 mm in length, and P. hassali is only 1.3 to 2 mm in length. The width is one third to one fifth the total length, increasing in inverse ratio. In certain species at the openings of the vaginae at the lateral or ventrolateral margins of the body, there are prominent swellings, the "Seitenwülste" of Zeller.

Organs of Attachment. The caudal disc bears on its ventral face the chief organs of attachment. These consist of suckers and hooks, the former arranged in pairs, three suckers on each side of the median line. The two posterior bothria are close together, those of the middle pair are separated by considerable distance, while the anterior pair may or may not be near each other. In all previously reported forms except P. alluaudi, the anterior suckers are separated by considerable

distance, giving the disc the shape described by Leidy as cordiform, (Fig. 37). In the single specimen of P. allenauli both the caudal and cephalic suckers are separated, while those of each side are contiguous. In P. orbiculare the anterior bothria are in the same close proximity as the caudal pair, and each sucker of the disc is separated from the two adjacent to it by uniform distances, making a perfect circle of bothria, (Fig. 1). In the six species studied by the writer, these suckers are complicated structures, set more or less deeply in the parenchyma of the caudal disc. Their structure, character of insertion, muscular attachments, and relation to surrounding tissue indicate that they are protrusible and retractile, and such movement may be observed by watching the live worm.

The suckers are cup shaped, (Fig.38), and in all the species described in this paper are constructed on an elaborate cuticular framework. As described by Zeller the sucker forms as a ridge around a larval hooklet, and later sinks into the parenchyma, and this method of origin explains the cuticular covering of the external and internal surfaces of the cup. Running across between these cuticular membranes, there are short refractive fibers which constitute the mass of the wall of the sucker, (Fig. 39). Wright and Macallum (1887) describing similar fibers in the walls of the suckers of Sphyranura say,"Instead of the substance of the sucker being formed of muscular fibers disposed in three directions, and capable of modifying the shape of the cavity, as in the distomes, it is not possessed of contractility in Sphyranura ( and probably in Polystoma), and is formed of prismatic fibers, rather

of a supportive than a muscular character, arranged perpendicularly between the concave and convex limiting membranes of the sucker." Goto (1894) described similar fibers in the suckers of Axine, Microcotyle, Octocotyle, Diclidophora, Hexacotyle and Onchocotyle and "considers them to be more of an elastic than a contractile nature". They are, he states, "different from the ordinary muscular fibers of the body and from those of the suckers of the Tristomidae and the Monocotylidae, as well as from those of the anterior sucker of Onchocotyle, both in optical characters and in reaction towards staining fluids." The structure of the suckers in these forms and their mode of operation is discussed by Goto at considerable length, but as the suckers he descfibed are constructed on a different type of cuticular framework from that present in the genus Polystoma, obviously the type of suctorial action is different.

In all the species described in this paper, the fibers which form the walls of the posterior suckers are similar to those described by Wright and Macallum and Goto; the cuticular framework is also flexible and elastic, but it is of a different type from that described by Goto. In the polystomes the sucker consists of three sections which may be designated as basal, intermediate and external or distal portions, (Fig.40). The external part or rim of the sucker is supported by numerous cuticular rods formed by the thickening at regular intervals of the cuticular lining. These rods are bent outward, their curvature maintaining the flare of the rim of the sucker. Distally they terminate just inside the rim of the cup and

basally they are continuous with and are processes from a band of cuticula which passes around the sucker and separates the external and medial portions. In toto specimens this band appears to be divided into sections that are almost square, each with a circular area in the center that increases and decreases in size as the focus is changed. Sections show that the cuticular lining of the sucker is folded outward against the convex wall with which it is fused, thus interrupting the continuity of the fibrous wall, (fig. 39). The two sides of this invaginated cuticular sac or ring are fused at regular intervals, leaving small pockets alternating with the places of fusion. These small openings in the cuticular band are conspicuous by reason of their different refractive index and show very plainly with a dark field illumination as the square or rectangular sections with the circular areas in the center, (Fig. 38). There is apparently no relation between the number of these sections of the cuticular band and the number of cuticular thickenings which serve as supports of the external section.

The middle section of the sucker extends basally from the previously described cuticular band to a somewhat similar evagination of the cuticular lining into the wall of the sucker, but this evagination does not extend to the external cuticular covering and only partially divides the fibrous wall. This middle or intermediate section of the sucker is supported by thickenings of the cuticular lining, processes that extend peripherally from the cuticular band which passes around the sucker at its base. These supporting ridges are not arranged

at regular intervals and they are much fewer in number than the cuticular rods which support the external section. They are often branched, tho not more than a single bifurcation was observed.

The basal portion of the sucker is circular, similar in structure to the portions previously described, it has internal and external limiting membranes with fibers extending between. At its center the cuticular and fibrous wall is interrupted and there is the structure described by Johnston as the connective tissue plug, which appears as a central disc or button, and to which the retractor muscles are attached. This central disc has thickened cuticular edges and bears the larval hooklet. Fig. 48 illustrates the method of operation of the suckers. Muscles are attached to the attached to the external wall of the intermediate and distal sections and the contraction of these muscles retracts the two external zones, with the accompanying protrusion of the basal part. Whether the small hooks at the bases of the suckers are functional is doubtful. As previously described, the cuticular supports do not extend quite to the external margin of the sucker, leaving a soft plastic edge which can be applied all the way around even on an irregular surface. With the contraction of the muscles attached to the basal disc, a vacuum is produced and forms a powerful means of adhesion. Since the walls of the sucker are non-contractile, and the bothria vary only slightly in size in a single species, the size of the suckers has been used by the writer as a character for determining specific

identity.

A cuticular framework similar to that present in Polystoma is described by Wright and Macallum for the suckers of Sphyranura osleri. They say, " As the wall of the sucker is itself destitute of contractility, another arrangement exists for modifying the shape of the cavity. Its wall is really divided into three concentric zones, which be special extrinsic muscles, can be worked independently. The two circular lines which separate these zones, are marked by an infolding of the investing membrane, which forms a sort of joint, permitting the independent movement of the zones."

In the collection of Professor H. B. Ward there is a single series of sections of P. integerrimum, and in this specimen the type of skeletal structure previously described is absent. Fig. 44 shows the character of the suckers in this form.

The caudal disc typically bears eighteen hooks. Sixteen are similar in size and shape, arranged six in a row between the anterior suckers, one situated at the base of each sucker, and four between the two posterior suckers. In addition to these hooks, there is a pair of great hooks, several times the size of the small hooks, between the two posterior suckers. The shape of these hooks and their arrangement is shown in Figs. 41 to 47.

The sixteen small hooks are present on the caudal disc of the larva before the suckers are formed and are called larval hooks by Willemoes-Suhm (1872), but Zeller (1876) says,

"Die sechszehn kleinen Häkchen mit ihren Oesen, welche der Haftscheibe angehoren und welche bei der Polystomum larvae so ausserordentlich deutlich zu erkennen ist, sind nicht, wie Willemoes-Suhm meint, nur 'Larvalorgane'. Sie werden nicht abgeworfen, sondern sind wie ich auf das bestimmteste wiederholen muss, bei der erwachsenen Thiere noch sämmtlich vorhanden, sehr beweglich und gewiss nicht ohne Bedeutung für ein festeres Anheften." Johnston (1912) in the description of P. bulliense says, "Four larval hooklets are present in a row on the ventral surface near the posterior edge of the disc or cotylophore. I have been able to find no trace either in the living worms or the fixed material, of the larval hooklets which P. integerrimum and other species bear near the anterior edge of the disc. There is a small anchor shaped hook in the base of each sucker. All these hooklets either disappear as the animal increases with age, or very readily become detached. In only one out of sixteen specimens have the whole four posterior hooklets been present; and in only two others were any hooklets at all to be seen. In all the other specimens no hooklets could be made out."

In my own material I find that the larval hooklets are invariably present in the bases of the suckers, but of the other larval hooklets, usually several are absent and often the ones present are so arranged that it is difficult to see how they could function in attachment. Those at the anterior edge of the caudal disc are seldom regularly arranged, and in many cases (Figs. 41-47) are in such irregular and unusual positions with reference to each other, that the use of one would interfere with the use of the others.

The great hooks are invariably present in the species in which the caudal disc is cordiform in shape, i.e. where the two anterior suckers are separated by a distance exceeding that between the two posterior suckers. In the species P. alluaudi and P. orbiculare the disc is circular and the great hooks are not developed. Usually the cordiform disc is wider and the circular disc is narrower than the body. At first it seemed possible to separate the genus into two subgenera, one in which the disc is circular and the great hooks are absent and another with a cordiform disc and great hooks present, but there seems to be no such clear line of separation. In P. orbiculare, one pair of the larval hooklets between the posterior suckers is somewhat larger than the others, and a large number of chitinous spicules are present on the disc, some between the suckers and others in the central area of the disc. In P. opacum the disc is practically intermediate in shape, it is difficult to determine whether it is circular or cordiform, and the great hooks are present altho they are not more than half the size of those in other species (Fig. 44). In P. hassali the disc may at times be circular and the great hooks are strongly developed (Fig. 34).

Body Covering. The body is covered with a non-cellular, unarmed cuticula, which is turned in at the external openings of the various systems. It does not have a uniform appearance but is traversed by lines which extend perpendicular to the surface of the body.

Musculature. As in all trematodes the musculature consists of the body wall composed of circular, longitudinal and two sets of oblique fibers; sets of longitudinal fibers that lie inside the body wall; and the dorso-ventral strands with much branched fibers which run thru the body at irregular intervals. The muscles of the body wall are delicate and scanty, not arranged in layers, but matted together in a sheet of muscle tissue. Sets of fibers pass from the body wall into the parenchyma at various places and either break up into smaller strands or are attached to the dorso-ventral sets. Posteriorly the muscles of the body wall are continued into and thru the caudal disc, and are inserted on the sides and in the bases of the bothria. Fiber strands from both sides of the body pass to each of the suckers, and smaller fibers from each sucker to the adjoining ones (Fig. 35).

Mesenchyma. The mesenchymal tissue of the body does not show a differentiation into ecto- and endoparenchyma as described by Brandes (1892) and other writers; it is not of a uniform character, but presents differences in appearance at different points in the same specimen. It may take the form of compact cellular tissue, or of vacuolated cells, or there may be large vacuoles apparently between cells, or the cellular structure may be entirely lacking there being only a reticulum of fibrous tissue. The parenchyma is traversed by many muscular strands, and the dorsal and lateral regions are occupied by the enormously developed vitellaria (Figs. 22-25).

Alimentary System. The digestive apparatus consists of a terminal anterior or mouth sucker, a pharynx and a bifurcate intestine. The anterior sucker is not an oral sucker, homologous with that of the distomes, but is merely an adhesive cup at the base of which is the opening into the pharynx. There is no limiting membrane separating it from the body wall, altho the membrane which forms its posterior limit and separates it from the body parenchyma bears some resemblance to the limiting membrane of the oral sucker of the distomes (Figs. 3,35). Branched muscle fibers pass from the body wall to the cuticula which lines the sucker. Johnston (1913) describes it as a weakly developed or incipient oral sucker. The anterior sucker and pharynx are lined with cuticula continuous with that of the external surface of the body.

The pharynx is approximately spherical, altho various states of contraction influence its shape to some extent. In most cases it opens directly into the intestine at the juncture of the right and left ceca. A short esophagus may be present in certain species (Fig. 4), and in others a short unpaired section of the intestine may extend anteriad from the bifurcation to the pharynx, (Fig. 36). The pharynx does not lie directly in the long axis of the body but obliquely, the posterior part is more dorsally situated than the anterior. In certain forms it appears to be constructed in two sections, there are lateral constrictions and a somewhat separated anterior portion (Fig. 3). Externally it is surrounded by a limiting membrane. In the species observed in this study, the pharynx is composed of non-nucleated, branched muscle fibers. Peripherally there is a

strongly developed layer of circular fibers extending around the organ from side to side, and penetrating among the circular fibers there are radial fibers which extend from the external limiting membrane to the cuticular lining of the pharynx. At the anterior end the circular fibers extend among the radial fibers from the periphery to the lumen, but posteriorly they are confined almost entirely to the external region (Fig. 37). Scattered among the fibers there are large nuclei, each with a deeply staining nucleolus. Each is surrounded by a granular or flaky area which is continued by a fine duct traceable by the presence of the same granular substance and which leads to the lumen of the pharynx. Goto described somewhat similar nuclei in the pharynx of *Diclidophora* and regards them as remnants of the cells that have produced the muscle fibers. The writer is inclined to the view that in *Polystoma* the granular or flaky substance is a secretion. No extra esophageal salivary glands were observed by the writer, but whether the secretion of the pharyngeal cells is salivary or not is still undecided.

There is wide variation in type of intestinal diverticula. In *P. integerrimum* the ceca are much branched and these branches ramify thru the caudal disc (Fig. 40). In *P. alluaudi* the ceca occupy the same location but are merely lobed and have no secondary branches. The two diverticula are united posteriorly. In *P. bulliense*, Johnston (1912) described "a diverticulum from the buccal cavity runs backwards, ventral to the pharynx, and for a distance equal to its length forming a median unpaired buccal pocket." In all other known species

there is a simple bifurcate intestine, the ceca terminating just anterior to the caudal disc. In two specimen of P. hassalli, however, the ceca are connected posteriorly, in one case the ends of the ceca are continuous and in the other there is a connexion some distance anterior to the ends of the ceca (Fig. 34). The walls of the ceca are composed of a delicate fibro-muscular tissue upon which rests the digestive epithelium. The epithelial layer consists of columnar cells whose nuclei lie near the fibro-muscular sheet and which have large rounded, often vacuolated bodies extending into the canal. The protoplasm of the cells is granular.

<u>Excretory system</u>. In this family as in all Heterocotylea, there are two excretory pores situated on the dorsal surface, about midway between the median line of the body and the lateral edge of the worm, near the level of the caudal margin of the pharynx, (Figs, 33,37). These open from vesicular expansions, which when filled are almost spherical, and when empty have folded walls. There may or may not be a small duct from the anterior duct opening into the vesicle. The descending collecting duct originates in the region of the pharynx from the fusion of smaller ducts and passes posteriad to the region of the caudal disc where it turns cephalad and continues as the ascending collecting duct to empty into the caudal side of the excretory vesicle. Both the descending and ascending ducts receive smaller branches at irregular intervals; at the caudal end of the body a canal joins the tubes of the two sides and a similar connexion occurs between the descending ducts just anterior to the pharynx. From this anterior communicating canal,

near the median line, a branch enters the anterior sucker. The excretory vesicles are lined with a thin layer of cuticula continuous with that of the external surface of the body and the collecting ducts and accessory branches have a fibro-membranous wall in which nuclei are ocassionally embedded. Zeller (1872) for P. integerrimum described many connections of the collecting ducts of the two sides thru anastomoses of their smaller branches. He also described cilia on the walls of the collecting ducts. Looss (1885) described the excretory system of P. ocellatum. He says the collecting ducts are not ciliated thruout but only in occasional areas, and described cilia in the capillaries. These capillaries are long and at the distal end are very much coiled. In this coiled part the capillary divides so that two flame cells discharge into each coil and are emptied by a single capillary. The caliber of the excretory vessels is very minute and altho varying somwhat as a result of distention, lacunar expansions were not observed. Because of the limited amount of material, much of which was received in a preserved condition, no attempt was made to trace the excretory system in living worms of this family. The vitellaria completely obscure the excretory ducts in toto preparations. The secondary ducts are so small and so often collapsed that it is impossible to follow their continuity with certainty in sections.

Nervous System. The morphology of the nervous system of P. integerrimum was described in detail by André (1910). He described a supra-esophageal brain from which three pairs of nerves pass anteriorly and three pairs pass posteriorly. The same author in another paper the same year gave a detailed description

of the eyes of P. integerrimum. No special technique was used to demonstrate the nervous tissue. The brain is the only part of the system differentiated. It contains large ganglion cells (Fig. 20).

Male Reproductive System. The testis is a branched and anastomosing structure in P. kachugae, in P. integerrimum it is lobed, and in the other known species it is oval or spherical. It is situated near or slightly anterior to the middle of the body. An internal vas deferens was described in P. integerrimum by Zeller, but Ijima (1884) traced the true relations of this tube and showed that it passes from the ootype to the intestine. This structure has been the source of much controversy and is is used by Odhner as the diagnostic feature separating the two groups of the monogenetic trematodes. The vas deferens arises from the dorso-cephalic margin of the testis and passes dorsad and anteriad. It extends dorsal to the cotype, between the dorsal margins of the ovary and uterus to the level of the genital pore. Here it turns ventrad and enlarges to form the seminal vesicle (Fig. 11). From the seminal vesicle a duct passes thru the cirrus sac, opening into the genital atrium (Fig.31). The vas deferens is small and has a fibro-membranous wall, the seminal vesicle has a lining of columnar epithelium, and the cirrus sac is composed of an external muscular wall enclosing a mass of parenchymous tissue. Ventrally the cirrus sac has a double invagination and the part between the invaginations bears the hooks of the genital coronet (Fig. 28). These vary in number and shape in the different species. With the contraction of the wall of the wall of the cirrus sac, the invagination

on either side of the genital coronet, provides for the extrusion of the genital papilla and the eversion of the hooks of the genital coronet. Stewart (1914) gives a diagram to illustrate the action of these spines as the cirrus is protruded and the points of the hooks project thru the genital pore.

Female Reproductive System. The ovary of P. kachugae is described by Stewart as "a curved sausage shaped organ, the curve forming all but a complete circle. The fundus is somewhat bulbous." In all other known species it is oval or comma shaped. It is situated a short distance anterior to the testis and in the same species may lie on either side of the body. In all the species studied by the writer it is comma shaped, the larger part is ventral, anterior and lateral, and the terminal part is dorsal, posterior and medial. The ova are formed in the large part and the ovary is divided into zones of growth, ova of increasing size are present in each succeeding zone (Fig. 30).

The vitellaria consist of masses of follicles occupying the dorsal and lateral regions of the body. Each follicle consists of several cells which may vary much in appearance, the lack of uniformity due to the secretive function of the cells. In the peripheral part of the body the cells are usually small, with granular or flaky protoplasm, a distinct nuclues and nucleolus, and those more centrally located may be two or three times their size, the extra-nuclear area either vacuolated or filled with droplets of the yellow vitelline substance. In some cells the vitelline droplets are scattered uniformly thruout the cell. The presence of the vitelline material in the

cells often renders the body so opaque that the diverticula can not be seen. The vitelline material is apparently identical with that which forms the shell of the egg, and this observation further confirms the statement of Goldschmidt (1909) that the vitellaria secrete the shell of the egg. Small ducts from the follicles (Fig. 6) unite and discharge into the longitudinal collecting ducts. These extend along the sides of the body lateral of the ceca and dorsal to the excretory tubules; on either side of the body there is an anterior and a posterior branch which unite just behind the level of the ovary and the common duct discharges into the external end of the vitello-vaginal canal. In P. bulliense, Johnston (1912) says, "The lateral vaginal swellings are formed by a large number of papillae, perforated by fine canals, which after a very short course, open into a fairly wide sperm reservoir, situated, one on either side, just under the swellings. From these reservoirs, a wide vaginal tube on either side runs backwards and inwards, to open into the anterior lateral yolk duct." A similar condition is described and figured by Zeller (1876) for P. integerrimum. In all other species in which the structure has been described, the vaginae are open funnels leading mediad and dorsad from the exterior and uniting just below the intestine with the common vitelline ducts to form the vitello-vaginal canals (Fig. 39). These tubes lead medially and unite, forming a duct which discharges into the cotype (Fig. 17) or they may open separately into the cotype (Figs. 16, 22).

From the ovary the oviduct passes posteriad and ventrad, opening into the ootype. Immediately anterior and dorsal to the opening of the oviduct, there branches from the ootype a small tube which coils about and opens into the intestine of the side in which the ovary is situated. This genito-intestinal canal is discussed in a previous section. The Mehlis' gland is never largely developed and is apparently lacking in some specimens. In others it is represented by a few nuclei which lie scattered in the parenchyma around the ootype. Zeller for P. integerrimum and Johnston for P. bulliense describe prominent "shell glands", and Stewart for P. kachugae described " a group of glandular cells found at the same transverse level as the ovary, but on the opposite side of the midline. They appear to be connected with the corresponding vagina, but their function is obscure." Since they are in the precise location of the Mehlis' gland, one is led to suspect that Stewart was confused in regard to the connections and relations of this group of cells.

The ootype is continued by a tube which passes anteriad on the opposite side from the ovary, and which leads to the uterus. Previous writers have called this tube the oviduct and Johnston (1912) says, " From the ootype, the oviduct runs forward to a point in front of the ovary, when it bends sharply backwards and runs in a straight course close to the ventral surface, almost to the level of the cotylophore, where it opens into the wide uterus." The use of the term oviduct for the tube leading from the ootype to the uterus is confusing and objectionable. Looss (1899) says, "Der Theil des weiblichen

Leitungsweges, der den Keimstock mit dem cotyp verbindet, ist der oviduct oder Keimgang," and this terminology is found in general use thruout the literature. In a large number of trematode genera the cotype opens directly into the uterus. In the Polystomidae however, there is a definite specialized tube leading from the cotype to the uterus. This duct is not homologous to the oviduct, is separated from that duct by the cotype, and further, in the specimens examined by the writer the histological character of the two are not the same. The epithelial lining of the oviduct is of the flattened type, and that of the second duct more columnar. Such a duct is present in many cestode genera and is called the uterine duct but since the question of the homologies of the female ducts in trematodes and cestodes is far from settled, there is a strong objection to the use of the cestode terminology. The term ooduct is proposed for the part of the female genital duct of the trematodes which is situated between the cotype and the uterus.

In P. bulliense the ooduct opens into the uterus not at the end but on the side, and there is a posterior uterine pocket. The uterus extends as a wide elongated sac from the extreme posterior end of the body to the common genital sinus. In P. alluaudi the intracecal area is occupied by the uterus and eggs are figured almost as far posteriad as the caudal union of the digestive ceca. In P. integerrimum there is a long uterus which extends in many coils anterior to the cotype, and contains a large number of eggs. In all other known forms the uterus is situated at the level of the ovary on the

opposite side of the body, and contains a single large egg or embryo. Zeller (1876) described a similar condition for the ectoparasitic form of P. integerrimum. Fig. 12 shows a very early embryo in which a shell is lacking and Fig. 30 a much later stage of development in which the embryo is enclosed in a shell.

In all the species studied by the writer, the tubes of the female system have a fibro-muscular wall and an epithelial lining. Where the oviduct arises from the ovary, at its union with the ootype and at either end of the uterine expansion, sphincter muscles produce short contracted portions of the tube. With the exception of the vitelline tubules, all the ducts have an epithelial lining which in the ootype, ooduct and uterus consists of tall columnar cells with distinct boundries and single nuclei. Describing the epithelial lining of the ootype in certin monogenetic forms Goto (1894) says that because of their appearance and reaction to stains he strongly suspects their glandular nature, but since a shell gland is present he can not understand their function. In certain species of Polystoma the Mehlis' gland is much reduced or absent, and in these forms the cells of the epithelial lining appear to be secretive (Fig. 10). This agrees with the present conception that the vitellaria secrete the shell substance and the Mehlis' gland the fluid in which the eggs are suspended.

The genital pore is situated on the ventral surface in the median line, just posterior to the bifurcation of the digestive tract. It opens from a common genital sinus (Fig. 31)

into which the uterus discharges and thru which the cirrus is extruded. The opening of the uterus is posterior and ventral while the cirrus sac opens into the dorsal part of the sinus.

Benham (1901) and Mac Callum (1913) state that copulation in polystomes has been observed only by Zeller (1873). When the two specimens of P. opacum from Trionyx ferox were placed in a watch glass, they soon came in contact and immediately started copulation, the cirrus of each worm was inserted in the right vagina of the other, and the two worms attached to each other both with the anterior suckers, and those of the caudal disc, tho only part of the posterior suckers could be brought in position for adhesion. Attempts to separate the worms failed, so an effort was made to fix them in the copulating condition, but they separated on the application of the killing fluid. This explains the statement of Johnston (1912) , "On one side only, in the specimens sectioned, was the vaginal tube filled with sperms; that on the other side was empty."

The following section contains a key for the identification of the species in the genus, the descriptions of four new species added to the genus, and additional information concerning the species P. coronatum Leidy and P. hassali Goto. The morphological comparisons establishing the specific identity of the new species are included at the end of each description.

## Key to the Species of the Genus Polystoma

A.(1) Uterus long, contains many eggs.

B.(1) Great hooks present on caudal disc.
- a. Ceca branching ..........P. integerrimum
- b. Ceca not branching .......P. bulliense

B.(2) Great hooks not present on caudal disc.
- a. ......................... P. alluaudi

A.(2) Uterus short, contains single egg.

B.(1) Great hooks present on caudal disc.
C.(1) Genital hooks equal length.
D.(1) Not more than 16 genital hooks.
- a. Genital hooks 8 in number,...... .....ectoparasitic form P. integerrimum
- b. Genital hooks 16 in number... P. hassali

D.(2) Genital hooks 32 in number.
- a. Bothria large, adjacent but not contiguous, pharynx smaller than anterior sucker... ............. ........P. coronatum
- b. Bothria small, widely separated, pharynx equal in size to anterior sucker..... ...................... P. microcotyle

D.(3) Genital hooks more than 32 in number.
E.(1) Testis simple.
- a. Bothria large, overlap...P. megacotyle
- b. Bothria small, separated.. P. ocellatum

E.(2) Testis branched.
- a. ...................... P. kachugae

C.(2) Genital hooks unequal length.
- a. ...................... P. oblongum

B.(2) Great hooks of caudal disc reduced or absent.
- a. Genital hooks 16 in number......P. orbiculare
- b. Genital hooks 32 in number .....P. opacum

## Polystoma orbiculare n. sp.

The material of this species consists of six specimens from the urinary bladder of Pseudemys scripta, from Raleigh, N.C., one specimen from the urinary bladder of Chrysemys marginata from Chicago, Ill., and two specimens from the urinary bladder of Chrysemys marginata from Creston, Iowa.

The body is an elongate oval, slightly more pointed anteriorly than posteriorly, and in two of the specimens with slight indentations of the body wall at the vaginae and at the posterior margin of the anterior sucker. These worms (Fig. 1) varied in length from 2.7 to 3.75 mm and in width from 0.9 to 1.2 mm. The caudal disc is circular, 0.8 to 1.07 mm in width, and bears the six acetabula arranged symmetrically in a circle. The bothria are approximately 0.2 mm in diameter, and are separated by regular equal intervals. With the exception of those at the bases of the suckers, no hooks could be found on the caudal disc. These are 0.016 mm in length and could be seen only under favorable conditions.

The anterior sucker (Figs. 2, 4) is 0.25 to 0.37 mm in length and 0.27 to 0.42 mm in width. It opens into the pharynx, a spherical structure 0.24 to 0.28 mm in diameter. There is a short esophagus visible in sagittal sections (Fig. 4) altho it is not distinguishable in toto preparations. The ceca meet anteriorly in a wide curve and extend as simple tubes almost to the posterior end of the body. They vary in caliber from 0.04 to 0.116 mm.

The testis is spherical or oval, usually slightly longer than broad, and measures 0.33 to 0.39 mm in width and 0.36 to 0.5 mm in length. It is near or slightly anterior to the middle of the body. The sperm duct arises at the anterior margin and passes anteriorly, dorsal to the ootype. Anterior to the ovary it turns ventrad and expands into a seminal vesicle. At the terminal end of the seminal vesicle the duct is encircled by a constrictor muscle, and then it passes as the ejaculatory duct thru the cirrus sac to open into the genital atrium (Figs. 11, 13). The cirrus sac is almost spherical, and consists of an external muscular capsule filled with parenchymatous tissue enclosing a central canal. In the dorsal part of the sac there are radial parenchymous muscles passing from the wall to the central duct, and among these fibers a few large nuclei. More ventrally there are sets of muscles developed around the central duct and these are connected to the wall of the sac. Externally the central canal terminates at the apex of a papilla which is separated by a deep depression from an evaginated muscular ring which bears the hooks of the genital coronet. This projecting muscular ring is separated from the wall of the cirrus sac by a second depression. These invaginations on either side of the genital coronet undoubtedly allow for the extrusion of the papilla and coronet of cirrus hooks on the contraction of the wall of the sac, while the muscles attached to the central canal and the muscular ring bearing the genital hooks serve as retractors. The genital coronet consists of sixteen hooks, similar in size and shape; they have an external sickle shaped part or shank which turns

outward and a basal part of about the same length embodied in the musculature (Fig. 15). The basal part is straight, near its union with the shank it bears many fine cuticular processes and the internal end is bifurcate. In the body parenchyma, around the terminal part of the cirris sac there are the large unicellular glands of the prostate (Figs. 13, 14).

The ovary is lateral and may be situated on either side of the body. It is 0.1 to 0.25 mm anterior to the testis. It is ovoid in shape, with the larger part in which the ova are being formed anterior and ventral, and the oviduct arising from the dorsal posterior region. It is marked into zones, larger and fewer cells are present in each succeeding zone. It is 0.1 to 0.148 mm in width, 0.14 to 0.185 mm in length and in one specimen cut in cross sections 0.175 mm in depth. The oviduct arises as a very small tube and immediately expands (Fig. 16). This expanded portion extends posteriad and ventrad and after a short constriction opens into the cotype, a specialized portion of the female tube where the vitello-vaginal canals are received and the genito-intestinal canal is given off. The genito-intestinal canal after two or three coils opens into the intestine of the side upon which the ovary is located. The vaginae are ventro-lateral in position and open to the exterior by funnel shaped mouths. The vitellaria occupy the lateral regions of the body from the pharynx to the posterior end and the dorsal region caudal to the testis. Collecting ducts run longitudinally, laterad of the ceca, and just below the cecum of either side

the common vitelline ducts unite with the internal end of the vaginae to form the vitello-vaginal canals. These canals open directly into the ootype, one on either side, and are thus continuous, forming a canal thru the body from side to side. The Mehlis' gland is represented by many nuclei which lie in the parenchyma around the ootype. The oöduct passes anteriad and lateral, on the opposite side from the ovary; it is smaller than the ootype in diameter and the epithelial lining is lower. After a slight expansion it is constricted and then opens into the uterus. The uterus contained a single egg or embryo. Fig. 12 shows a morula like mass of cells not enclosed in a shell and in five of the specimens there are large spherical eggs which vary from 0.21 to 0.24 mm in diameter.

The excretory system shows no departure from the typical form, and while it can not be completely followed in sections, the larger ducts occupy the characteristic positions. The descending collecting ducts arise in the region of the anterior sucker and pass posteriad, lateral and ventral to the ceca. They wind back and forth in short curves, forming a wavy line, and at the posterior end of the body they turn anteriad and pass in the same winding course to the excretory vesicles. Both descending and ascending ducts receive small branches at irregular intervals. The excretory pores are lateral and dorsal, at the level of the bifurcation of the intestine. (Fig. 5).

This species agrees with P. alluaudi in shape of caudal disc and absence of great hooks, but differs from that species in type of uterus, number of hooks in the genital

coronet, and in character of the intestinal diverticula and testis. P. orbiculare agrees with P. hassali in the number of genital hooks, but the hooks are very different in size and shape; P. hassali has the great hooks of the caudal disc well developed and they are absent in this species. In certain particulars P. orbiculare resembles P. opacum but the two species have different numbers of hooks in the genital coronets; they differ also in the relative size of caudal suckers. The great hooks of the caudal disc are present in P. opacum, and the two species differ in that one is parasitic in the urinary bladder and the other in the oral cavity.

Polystoma opacum n. sp.

Two worms of this species were obtained from the esophagus of a single specimen of Trionyx ferox from Newton, Texas, and another from the esophagus of Malacoclemmys lesuerii from the same region. These trematodes were the same color as the lining of the esophagus and so firmly attached that they were removed only with great difficulty.

The worms (Fig. 18) measured 4, 3.75 and 3.25 mm in length and 1, 0.85 and 0.8 mm respectively in width. The body has an elongate oval outline, is flattened dorso-ventrally, and observed in living condition great variations in shape were noted. In an extended condition it narrows at either or both ends, and the contracted form may be not more than half the length when extended, and be broadly oval or quadrate in shape. The caudal disc is slightly wider than the body in the mounted specimens, measuring 1.09 and 1.21 mm in width while each sucker is approximately 0.4 in diameter. The bothria have a chitinous skeletal framework as described in the generic discussion. In the external meridianal band there are thirty two divisions, which number corresponds with the number of hooks in the genital coronet. The bothria are arranged in a circle altho the anterior pair are separated by a distance slightly exceeding that of the posterior bothria. Between the anterior suckers there are many chitinous spicules, and in one specimen two of the larval hooks. Chitinous spicules are present on the sides of all the bothria and over the ventral surface of the disc. Between the posterior bothria there are three pairs of hooks, two pairs of the small larval hooks and one larger pair,

but the great hooks are relatively much smaller than the corresponding structures in other species in which they are present. The larval hooks are 0.007 to 0.009 mm in length and the great hooks are 0.075 mm in length. The chitinous spines present on the disc have no definite arrangement and their points may stand in any direction, the three larval hooks between the anterior suckers of one specimen have no definite relative position and their hooks point in different directions, those at the posterior edge of the disc are set in a row at more or less regular intervals and their hooks all point backward.

The cuticular covering of the body is about 0.014 mm in thickness, and on the contraction of the body is thrown into minute folds and furrows.

The anterior sucker is oval, 0.2 to 0.22 mm in length and 0.27 mm in width. It opens into the pharynx (Fig. 19), a spherical structure 0.3 mm in diameter. There is a broad nerve commissure crossing the anterior part of the pharynx which contains large ganglion cells (Fig. 20). From this dorsal commissure a nerve passes ventral on either side of the pharynx.

The digestive tract is of the triclad type, the pharynx is followed by a short esophagus, 0.17 mm in length in the sectioned worm and the diverticu;a extend as simple tubes almost to the posterior end of the body. They are about 0.15 mm in diameter, and terminate blindly dorsal to the middle pair of bothria (Fig. 25). The ceca are lateral in position but close together, separated by only 0.3 to 0.25 mm. They have the usual fibro-muscular coat and epithelial lining,

and were empty in the sectioned individual.

The testis is spherical, 0.4 to 0.5 mm in diameter, situated in the median line of the body. It is slightly anterior to the middle of the worm and is composed of a large number of lobes or strands of cells, compacted and enclosed in a membranous capsule. Cells with the chromatin of their nuclei in all stages of division and mature spermatozoa were observed in sections. The sperm duct arises at the anterioe dorsal margin of the testis and curves dorsad and cephalad. Anterior to the uterus it turns ventrad and expands to form the seminal vesicle. From the seminal vesicle a small ejaculatory duct leads thru the cirrus sac and opens into the common genital sinus (Figs. 22, 23).

The ovary is ovoid or comma shaped, situated a short distance anterior to the testis, and all three specimens is located on the left side of the body, but since in other species it may occur on either side, it is probable that the examination of a larger number of individuals would show specimens with the ovary on the right side. In dorsal view it is from 0.16 to 0.2 mm in length and 0.08 to 0.12 mm in width, while in the specimen that was sectioned it is 0.08 mm in width and 0.3 mm in depth. The oviduct arises at the dorsal posterior margin and curves posteriad, mediad and ventrad where it opens into the ootype. The vitello-vaginal canals open separately into the ootype just below the origin of the genito-intestinal canal. This latter duct after two or three coils opens into the intestine of the side in which the ovary is located. The ooduct passes to the right side of the body dorsad and anteriad, where it opens into the uterus. Mehlis' gland is present altho not well

developed and the cells are scattered along the oöduct as well as around the ootype altho they are not so numerous in the former location. The vaginae open to the surface on either side, at the ventro-lateral margins of the body, at the level of the posterior margin of the ovary (Fig. 22). From the vaginae, canals pass inward and each receives just below the cecum a duct from the vitellaria of that side. The vitello-vaginal canals form a tube leading thru the body from one side to the other. The vitellaria consist of large compact follicles underlying the entire dorsal surface of the body from the pharynx to the caudal disc, except the region over the uterus. They are so extensively developed that they obscure the internal structures and render the body opaque, and this character suggested the name of the species. Common collecting ducts run longitudinally along the body, lateral to the intestinal diverticula, and these discharge into the vitello-vaginal canals as previously described. In each of the specimens there is a single large egg in the uterus, and in the one sectioned the uterus extends cephalad of the pore and to a point 0.03 mm from the bifurcation of the intestine. The eggs are broadly oval, 0.25 mm long by 0.2 mm wide. The shell is yellow, refractive to light and apparently composed of the same substance that occurs in small droplets in the vitellaria.

The uterus and cirrus sac open into the genital sinus, the opening of the cirrus is anterior and dorsal to that of the uterus. The common genital pore is situated in the median line about 0.12 mm caudad of the bifurcation of the intestine. Embedded in the wall of the cirrus sac and with their points

forming the so called coronet the genital hooks in appearance suggest the corolla of a flower. There are thirty three of these hooks in one mounted specimen and thiry two in the other, and in entire length they measure 0.05 mm. the projecting part comprising about half the total length.

P. opacum agrees with P. allmaudi and P. orbiculare in the shape of the caudal disc and in the reduction of the great hooks of the caudal disc, but P. allmaudi has only three spines in the genital coronet, and a long post ovarian uterus which contains many eggs. P. orbiculare has a larger anterior sucker, smaller caudal bothria, smaller pharynx, fewer vitelline follicles and only half as many hooks in the genital coronet. P. opacum differs from P. coronatum and P. microcotyle in the shape of the caudal disc and in the reduced condition of the great hooks of the disc.

## Polystoma megacotyle n. sp.

The material of this species consists of three specimens from the mouth of Chrysemys marginata, from Creston, Iowa. One worm was cut into cross sections and the other two mounted as stained toto preparations.

These worms (Fig. 26) have an elongate ovoid shape. Widest in the region just anterior to the caudal disc, they gradually become narrower anteriorly and posteriorly they taper rapidly to a narrow caudal tip which is set in the antero-central part of the caudal disc. The worms are 2.5 to 2.7 mm long and 0.71 to 0.78 mm in width. The caudal disc is cordiform and the bothria are so large that they slightly overlap each other. The suckers are arranged in about four fifths of a circle around the lateral and caudal margins of the disc. Lateral measurements thru the disc at the level of the cephalic suckers are from 1 to 1.4 mm, thru the middle bothria 1.2 to 1.8 mm, and thru the caudal bothria 0.68 to 0. 7 mm. The disc bears the characteristic armature of hooks. Across the anterior margin of the disc there are three larval hooklets in one specimen and four in the other , but their arrangement is not regular or definite and their position would indicate that they do not function in attachment. In the specimen reproduced in Fig. 26 the two hooks of the right side have their points almost together and their bases apart. In the bases of the suckers there are small larval hooklets, and one pair similar in size and shape between the two caudal bothria. Also between the posterior suckers there is the pair of great hooks and a pair of hooks intermediate in size between the great and larval hooks.

The hooks measure in size, larval 0.017 mm, great hooks 0.118 mm, and the pair intermediate in size 0.058 mm.

The cuticular covering of the body is approximately 0.005 mm in thickness on the dorsal and 0.003 to 0.004 mm in thickness on the ventral surface. It is turned in at the external openings and lines the digestive tract to the bifurcation.

The anterior sucker is set off from the remainder of the body by a slight constriction. It is oval, its longest axis crosswise of the body, somewhat flattened posteriorly, and measures 0.28 mm in length by 0.35 to 42 mm in width. It is followed by the pharynx which is 0. 35 to 0.38 mm long, 0.38 to 0.44 mm broad and in the sectioned worm 0.34 mm thick. There is no esophagus, the ceca meet anteriorly in a wide curve and extend almost to the posterior end of the body. They are 0.06 to 0.11 mm in diameter, and have an epithelial lining 0.017 to 0.035 mm in thickness set upon a fibro-membranous base. The vitellaria are so thich the diverticula can not be traced in toto preparations.

The testis is situated near the center of the body, it is spherical or oval, 0.28 mm to 0.35 mm long, 0. 35 to 0.38 mm wide, and in the sectioned worm 0.28 mm thick. The course of the vas deferens and the character of the male organs is similar to that in the previously described species (Fig. 31). The genital coronet contains thirty six hooks in one and forty two in the other toto specimen. They are similar in size and shape, have a straight basal portion with a bifid end which is embedded in the wall of the cirrus sac, and a sickle shaped shank which projects into the genital atrium. The basal portion is the same

length as the shank and each part measures 0.03 mm.

The ovary is a broad comma shaped organ, situated about midway between the pharynx and testis, on either side of the body. The larger part is anterior and ventral and contains many nuclei of forming ova, and there are zones of developing ova each with larger and fewer cells till dorsally and posteriorly the oviduct is given off. (Fig. 30). The oviduct passes mesiad, expanding slightly, and then posteriad and ventrad to open into the ootype. This structure is in the ventral part of the body just anterior to the testis, from the sides it receives the vitello-vaginal canals and gives off the genito-intestinal canal. The genito-intestinal canal after three sigmoid flexures opens into the intestine on the same side as the ovary. It was empty in the sectioned worm. The external openings of the vaginae are situated on small prominences," Seitenwülste", ventro-lateral in position, altho there is a single large opening to the exterior. The vitellaria consist of masses of follicles occupying the dorsal and lateral areas of the body, extending from the pharynx to the caudal disc. They form a sheet of gland cells on the dorsal side of the body posterior to the testis, and anteriorly they occupy chiefly the lateral areas and are much reduced in the median field. On either side, at the level of the ootype, a common duct from the longitudinal collecting ducts passes ventrad and just below the cecum unites with the vagina of that side to form the vitello-vaginal canal which discharges into the ootype. The ooduct leads to the uterus, which in each of the specimens contained a large egg. A section of the egg is shown in Fig. 30. The eggs are oval,

0.15 by 0.18mm and in the sectioned worm the egg is 0.24 mm in depth. From the uterus a small duct leads anteriad and ventrad, opening into the genital atrium ventral to the cirrus sac.

The excretory system agrees with the general description given. The descending and ascending ducts are 0.006 to 0.011 mm in diameter, when empty their walls collapse.

P. megacotyle differs from all known American forms in the large number of hooks present in the cirral coronet, and in this character agrees only with P. ocellatum. The species differs from P. ocellatum however, in the difference in size of the anteriorsucker and pharynx as well as in size of the caudal bothria. P. megacotyle differs from P. microcotyle in the number of genital hooks and in the size of posterior suckers. P. megacotyle has a larger pharynx, larger caudal bothria and a larger number of genital hooks than P. coronatum.

Polystoma microcotyle n. sp.

This species is described from a single specimen from the mouth of Chrysemys marginata of Creston, Iowa. The worm was stained and mounted in toto (Fig. 32).

It is 3 mm long, in shape an elongate flattened oval, 0.78 mm in width. The caudal disc is cordiform, 1 mm in width at the level of the anterior suckers, 1.07 mm thru the middle pair and 0. 74 mm thru the caudal pair of bothria. Each bothrium is 0.28 mm in diameter, and with the exception of the longer distance between the anterior suckers, they are separated by almost regular equal distances. Four larval hooklets are present between the two anterior suckers, three in a row but with their hooks pointing in three different directions, and the fourth some distance posterior to the others on the other side of the disc (Fig. 35). Between the posterior suckers there are three pairs of hooks; the pair of great hooks, one pair of larval hooks the same size and shape as those at the anterior margin of the disc and those at the bases of the suckers, and the third pair is intermediate in size between the great hooks and the larval hooks. This third pair of hooks are the same shape as the great hooks. The larval hooks are 0.017 mm long, the great hooks are 0.116 mm long and the pair intermediate in size are 0.061 mm long.

In this specimen the musculature of the caudal disc shows very plainly (Fig. 35). The muscles of the body wall converge at the posterior end of the body and pass into the caudal disc, breaking up into six chief sets, one of which is inserted into the base of each bothrium. Smaller muscle fibers

pass from each sucker to all the other suckers.

The anterior sucker is 0.2 mm long and 0.42 mm wide; the pharynx is 0.4 mm wide and 0.37 mm long. No esophagus is visible in the toto preparation and only the anterior part of the intestine can be seen.

The testis is slightly anterior to the middle of the body; it is oval, 0.36 mm in length and 0.42 mm in width. The sperm duct can be traced dorsally and anteriorly; cephalad of the ovary it expands into a seminal vesicle which stain deeply due to the presence of spermatozoa. The genital coronet contains thirty two hooks, equal in size and similar in shape.

The ovary is on the left side of the body, about midway between the testis and the genital pore. The oviduct arises at the median posterior margin and passes mediad, but the structure of the cotype could not be made out. The uterus can be distinguished at the level of the ovary on the opposite side and is empty. Laterally the vaginae are visible and the vitello-vaginal canals may be traced medially a short distance from the ceca. The vitellaria are strongly developed, extending from the pharynx to the posterior part of the body and obscuring the ceca caudal to the testis. No vitelline ducts were seen.

The excretory vesicles appear one on either side of the body, dorsally, at the level of the bifurcation of the intestine.

In number of genital hooks, this species agrees only with P. coronatum Leidy. A comparison with a type specimen of P. coronatum shows that in P. coronatum the pharynx and testis are much smaller and the bothria of the caudal disc are much larger.

Polystoma coronatum Leidy

This description is from a single type specimen from the United States National Museum. The worm was stained and mounted in toto.

Leidy (1888) says the host is the common food terrapin, and the previous year, speaking of eating terrapin he mentions Emys palustris and Emys rugosa. Braun (1890) lists the species from Cistudo carolina. Goto (1899) concerning the specimen described by Leidy as P. oblongum, refers to the food terrapin as E. rugosa.

Leidy gives no figure and his description states; " Polystomum coronatum. .. Body when elongate lanceolate. Caudal disc wider than the body, cordiform, with three pairs of bothria and with body attached between the anterior two pairs; changeable in form to oblong, circular or quadrate; with three pairs of minute hooks between the anterior pair of bothria and with a larger pair and two smaller pairs between the last pair of bothria. Genital aperture with a circular or transverse oval coronet of 32 hooks of equal length. No eyes visible. Length, elongated from 4 to 6 mm; contracting to about half the length and widening proportionately."

The specimen from which the present description is made (Fig. 37), is 3.15 mm long and 0.83 mm in width. The greatest width is at the level of the vaginae, the body tapers rapidly anteriorly, widening again slightly at the anterior sucker. From the level of the vaginae the body gradually grows narrower posteriorly to its insertion into the caudal disc. The disc is 1.24 mm wide at the level of the anterior suckers, 1.2 mm

thru the middle pair and 0.78 mm wide thru the caudal pair of bothria. Each sucker is approximately 0.17 mm in diameter, and constructed as previously described. There are thirty two small divisions in the peripheral cuticular band of the only sucker in which they could be counted. The disc bears the usual eighteen hooks, the six larval hooklets at the anterior margin of the disc are situated in a row equidistant from the anterior edge of the disc, the two lateral hooks on either side are nearer each other than the more centrally located one side is to the median one of that side. Larval hooklets are present in the bases of the suckers, and one pair of similar hooks is present between the caudal bothria. Between the caudal suckers there are also present a pair of great hooks and third pair intermediate in size between the other two. The larval hooklets are 0.02 mm in length, the hooks of intermediate size are 0.051 mm in length and the great hooks are 0.132 mm in length.

The anterior sucker is oval, 0.16 mm long and 0.4 mm wide; the pharynx is circular in outline, 0.3 mm in diameter. No esophagus can be seen in the toto preparation and the ceca behind the posterior margin of the testis are obscured by the vitellaria.

The testis is slightly anterior to the center of the body, circular in outline, and 0.3 mm in diameter. The vas deferens could not be distinguished; the cirrus sac in ventral aspect is 0.19 mm in diameter, the genital coronet contains thirty two hooks similar in size and shape.

The ovary is situated on the right side of the body, about its own diameter anterior to the testis, in ventral view

it is circular, 0.094 mm in diameter. The oviduct passes posteriad and mediad, and the ootype appears as a darkly stained area. The vaginae can be distinctly seen and laterad of the ceca on either side there is a large cavity communicating with the exterior. The uterus is empty, the folded walls of the cavity are visible on the left side of the body. The vitellaria are strongly developed, masses of follicles render the posterior part of the body opaque. Anteriorly they extend to the region of the pharynx, but are largely interrupted in the intracecal area cephalad of the testis and the structures in this region may be discerned. None of the vitelline ducts are visible.

The excretory vesicles are anterior to and slightly laterad of the ceca at the level of the caudal margin of the pharynx, but no ducts could be seen.

Polystoma hassali Goto

This species was described by Goto (1899) from the urinary bladder of Cinosternum pennsylvanicum from Maryland. The writer has collected the species from other hosts and localities. A single specimen was found in the urinary bladder of Aromochelys carinatus from Newton, Texas; five were collected from the urinary bladder of Aromochelys odoratus from Raleigh, N. Carolina; two from the urinary bladder of Cinosternum pennsylvanicum from Raleigh, N. C.; and three from the urinary bladder of Chelydra serpentina from Walker, Iowa.

These worms (Figs. 34, 36) vary from 1.3 to 2 mm in length and from 0.4 to 0.65 mm in width. The caudal disc varies in shape from hexagonal to cordiform and is of approximately the same width as the body. The suckers are 0.12 to 0.18 mm in diameter. The eighteen hooks of the caudal disc have the usual arrangement and are described by Goto. However, he reports the larval hooks as being 0.33 mm in length, and the great hooks between the caudal bothria as 0.125 mm in length. This is evidently a typographical error, since he figures the great hooks as about four times the size of the small ones. In the present material the great hooks are the same length as stated by Goto and the smaller ones are 0.033 mm in length which agrees with the figures of Goto by a change of one place in the decimal point.

The anterior sucker is ovoid, more pointed anteriorly. It may be longer in either the antero-posterior or lateral axis, and varies in diameter from 0.22 to 0.33 mm. The pharynx is spherical or oval and varies in width from 0.1 to 0.14 mm ; it may be longer in either axis. There is no esophagus but in some

specimens a short unpaired section of the intestine extends anteriad from the bifurcation to the pharynx. In others, and this is the more usual condition, lateral pockets of the intestine extend anteriad, one on either side of the pharynx (Fig. 33). The anterior sucker and pharynx are lined with cuticula; the intestine with the usual digestive epithelium. In those specimens in which the uterus contains an egg, the large size of the egg causes the ceca to be widely separated at the uterine level and they approach each other behind the uterus. In one specimen, median branches from the two ceca fuse and form a caudal connexion of the diverticula (Fig. 34), and in another the two ceca are united at their ends.

The testis is situated ventrally, just behind the middle of the body; it is a somewhat shapeless mass, roughly oval in outline, cross wise of the body, extending between the ceca just posterior to the uterus. The vas deferens passes anteriad, dorsal to the ovary and between it andthe uterus; anterior to the uterus the sperm duct turns ventrad, enlarges to form a seminal receptacle, and then passes thru the cirrus sac, opening into the genital atrium (Fig. 17). The genital hooks are sixteen in number, 0.028 mm in length, straight, and with wing like processes at the middle as described by Goto.

The ovary is comma shaped or ovoid in outline, situated obliquely in the body, on either the right or left side. Typically the ovary is on one side of the body and the uterus on the other, but the enormous size of the egg causes the uterus to occupy a more or less central position, crowding the

ovary far to one side. The ovary is 0.058 by 0.075 mm in the smallest and 0.085 by 0.12 mm in the largest worms, altho the size of the ovary does correspond absolutely with the size of the worm. The oviduct arises at the dorsal, median and posterior part of the ovary and after a loop dorsally it turns posteriad and ventrad to open into the ootype. Mehlis' gland is present. The genito-intestinal canal branches from the ootype and after a short winding course opens into the intestine near the ovary. From the ootype, the oöduct passes laterally to the opposite side of the median line and then anteriorly and dorsally to open into the dorsal posterior part of the uterus. The vitellaria extend from the pharyngeal region to the anterior margin of the caudal disc, and as described by Goto," lobes not very numerous, separated from one another, mostly confined to the lateral portion of the body, but also present in the median portion behind the testis". The vaginae are situated laterally, midway between the anterior and posterior ends of the body. There are no vaginal prominences, the vaginal openings are single, and internally they unite with ducts from the longitudinal vitelline canals to form the vitello-vaginal canals, as described for the other species. They do not open separately into the ootype, but the two vitello-vaginal canals open into a common reservoir from which a duct passes dorsally and discharges into the ootype (Fig. 17). In a few of the specimens the uterus is empty and in others contains a single large egg, the size of which varies between wide limits. The smallest eggs are 0.11 by 0.25 mm and the largest 0.18 by 0.34 mm. The posterior edge

of the uterus is at the level of the vaginae, and anteriorly there is a small duct from the uterus to the ventral posterior part of the genital atrium. The genital pore is in the median line, a short distance posterior to the bifurcation of the alimentary tract.

The excretory pores are slightly more caudad than in the previously described species. Descending and ascending ducts occupy the usual positions.

## IV. Aspidogastridae

In 1856, the same year that Leuckart proposed the division of the trematodes into the two families Distomea and Polystomea, Burmeister separated Aspidogaster from the remainder of the trematodes on the basis of the adhesive apparatus, and suggested a division of the group into, Pectobothrii for the polystomes, Aspidobothrii for Aspidogaster, and Malacobothrii for the distomes. This is the basis of classification followed by Monticelli (1892) when he divided the group into the three suborders Heterocotylea, Aspidocotylea and Malacocotylea.

The Aspidocotylea contains the single family Aspidogastridae, or as it was formerly known, Aspidobothridae. The change was proposed by Poche (1926) to make the name of the family agree with the rules of zoological nomenclature. In Art. 4 of the International Rules of Zoological Nomenclature as approved by the Ninth International Congress, Monaco, 1913, there is the statement, "The name of the family is formed by adding the ending -idae, and the name of the subfamily -inae to the stem of the name of its type genus."

The family is of special interest to students of trematode morphology. The form of the adhesive apparatus with its retractile marginal organs, the separation of the body into dorsal and ventral portions by a muscular partition, the sac like alimentary tract, and the details of the genital organs are peculiar to the group. The family contains both ecto- and endoparasitic species, forms with a direct development and at least one species which has an intermediate host, while the hosts infested by the adult parasites include both invertebrates

and vertebrates, species having been reported from molluscs, fishes and turtles.

Revisions or summaries of the group have been made by Diesing (1859), Taschenberg (1879), Hoyle (1888), Monticelli (1892), Braun (1893), and Nickerson (1902).

Only two genera of the family are known from North America, Aspidogaster von Baer 1827 and Cotylaspis Leidy 1856. The material which furnished the basis of the present study consisted of specimens of Aspidogaster conchicola, Cotylaspis insignis and Cotylaspis cokeri. The first two species are well known and have been described in detail, so further description is unnecessary. The last species has been reported but once, by Barker and Parsons (1914), and since their article is merely a preliminary report the species is described in detail.

Aspidogaster conchicola von Baer.

About fifty specimens from the pericardial and renal cavities of Anodonta corpulenta from Havana, Illinois, and a similar number of specimens from the same organs of Quadrula undulata from North Judson, Indiana, constitute the material of this species available for study.

A detailed comparison of these apecimens with the descriptions of Aspidogaster conchicola as given by Voeltzkow, Stafford and others, confirms their specific identity and substantiates the observations of Leidy (1851), Kelly (1899) and Kofoid (1899), that A. conchicola occurs in this country, and so far it is the only species in the genus known from molluscan hosts.

Kelly (1899) examined 1537 individuals of forty four species of unios from Mt. Vernon, Iowa, Havana, Illinois, and Lewisburg and Phoenixville, Pennsylvania for parasites and includes in his report results of the examination of 77 individuals belonging to eighteen species, made by Dr. Kofoid in 1895 and 1896. A. conchicola was found in 435 cases in the pericardium only, in 75 in the kidneys only, and in 134 cases both cavities contained the parasite. He says the presence of the mature trematode in the pericardium and of eggs within the nephridia is not infrequent. Of the 1537 specimens examined, 41% were parasitized with A. conchicola and 37 of the 44 species were infested with the parasite.

Cotylaspis insignis Leidy

The material of this species consists of specimens from Anodonta imbecilis, A. corpulenta, Lampsilis gracilis and Unio pustulosis from Havana, Ill., and others from Anodonta ferrus and A. ovata from Reed's Lake, near Grand Rapids, Michigan. The material proved to be of a single species and identical with C. insignis Leidy.

Leidy first discovered the parasite in the Unionidae of the Schulykill River and founded the genus to receive the new species. His (1858) generic and specific diagnosis follows: " Body curved infundibuliform, anteriorly cylindro-conical, posteriorly expanding into a subcircular or oval ventral disc with numerous acetabula arranged in a triple series. Mouth infero-terminal, with prominent upper lip, and protractile into a cup or disc like acetabulum. Intestinal apparatus as in Aspidogaster, eyes two, distinct, black, situated on either side of the head. Generative apertures inferior, between the head and ventral disc." C. insignis, type species, is, " Translucent white or pink white, upper lip snout like, conical, ventral disc crenate at the margin: acetabula 39, oblong quadrate, the outer rows continuous in front and behind forming a circle. Length from ½ to 1 line; ventral disc from ¼ to ½ a line in diameter. Adheres to the outer surface of the renal organ and upper margin of the foot, within the cleft of the upper branchial cavity of Anodonta fluviatilis and A. lacustris."

Forbes (1898) reports this parasite in the river clams at Havana, Illinois.

Osborn (1899) described the species from Lake Chautauqua, New York as Platyaspis anadontae.

Kofoid (1899) corrected this error, demonstrated that Leidy's genus is entitled to recognition, and established the specific identity of C. insignis Leidy and Platyaspis anadontae Osborn.

Kelly (1899) reporting on the examination of over 1600 individuals of forty four species of Unionidae, found the parasite in twenty four different species of molluscs and present in an infection of 18%.

Osborn (1904) gives a review of the literature, an account of the distribution, habits, external and internal anatomy of the mature worm and the description of a very young individual. The young specimen is described with single ventral sucker, no eye spots, no marginal organs, two entirely distinct excretory systems and wholly separate pores. This condition of the excretory system is compared with the condition in redia and cercaria and a suggestion is made, altho credited originally to Leuckart, that the Aspidogastridae are sexually mature redia.

Cotylaspis cokeri Barker and Parsons

This species was described by the writer as Cotylaspis rhadina n. sp. in a thesis submitted in partial fulfillment for the degree of Master of Arts in the Graduate School of the University of Illinois in June 1914. The following October Barker and Parsons published a brief description of the species naming it C. cokeri. Since the description of Barker and Parsons is not only meager but inaccurate in many particulars, the species is described here in detail.

From four to twenty five specimens were found in each of seven specimens of Malacoclemmys lesueurii from Newton, Texas.

The worms (Fig. 50, 51, 52) average 1.5 mm in length by 0.7 mm in width altho there is considerable variation in relative length and width due to the movements of the animal. The body is composed of two parts, an anterior forebody and a posterior ventral adhesive disc. When extended the forebody has the shape of a cornucopia, the larger end attached obliquely to the central two thirds of the dorsal surface of the adhesive disc. Extended it manifests an elongate form, projecting beyond the adhesive disc a distance equal to the length of that structure; in a retracted condition it is compact and may not project beyond the disc. The total length of the worm varies therefore with the state of extension of the forebody, from the length of the adhesive disc to twice that distance.

The adhesive disc (Fig.51) is a muscular organ, a multi-loculate sucker, used for attachment and locomotion. It has a crenate oval outline, the dorsal surface is arched and the ventral surface is flattened. There is a limiting membrane

separating the musculature of the disc from the parenchyma of the body (Figs. 54, 57). The ventral surface is divided by two longitudinal and eleven cross ridges into thirty two acetabula, which are arranged in three rows, there is ten median and twenty two peripheral alveoli. These compartments change in shape with the movements of the animal, becoming oval or quadrangular. The shape and size of the disc are relatively constant, measurements of the disc in twenty mounted toto specimens vary only from 1.2 to 1.4 mm in length and from 0.59 to 0.78 mm in width. Since in functional capacity and superficial form, this structure recalls the molluscan foot, it has often been termed the foot altho the morphological comparison is not precise.

Movement consists of extension and retraction of the forebody, which may be turned in any direction, and in the less striking and more restricted movement of the disc. The disc has a tendency to turn up at the edges, especially at the anterior and posterior ends. In adhesion the organ may act as a unit, or the separate alveoli may function independently. In locomotion there is a regular series of movements, the forebody is extended and attached by the sucking action of the mouth funnel, then the disc is loosened and the forebody contracted, bringing the anterior part of the disc near the mouth, when the disc is attached and the series of movements repeated. The worm moves rapidly across the field of the microscope.

Body covering. Externally the worms are covered by a non-cellular cuticula, which is thickest on the dorsal side of

the body and thinnest on the ventral surface of the adhesive disc. It is without hooks or spines, and on the dorsal surface reaches five micra in thickness while on the ventral face of the disc it is only one micron in thickness. The cuticula is turned in at the external openings and lines the external portions of the canals of the alimentary, excretory and reproductive systems.

Musculature. Immediately inside the cuticula is the three layered dermo-muscular wall, circular, longitudinal and oblique muscles occurring in the order mentioned, the circular lying next to the cuticula, and in all parts of the wall being better developed than the others. In some places the longitudinal and oblique muscles are very scanty. The musculature of the body wall of the ventral side of the forebody is continued posteriorly in a thin sheet, forming the so called septum (Fig. 57), which lies just above the limiting membrane of the musculature of the disc and which extends posteriad as far as the caudal end of the cirrus sac. The parenchymous muscles of the body are long, often much branched, and most abundant in locations where they connect different parts of the body wall with each other or with adjacent internal structures. In the anterior part are many well developed muscles used in the movement of that region. Running longitudinally among the vitellaria, as well as dorso-ventrally among the viscera there are many muscle fibers. Sphincters and dilators occur at the genital pore, excretory pore, at the base of the mouth funnel, and at the opening between the pharynx and the intestine. As previously mentioned, the adhesive disc is separated from the forebody by a limiting membrane (Figs.54,57). This membrane runs parallel to the

general course of the external, ventral surface of the disc, projecting ventral at each ridge. Extending between the membrane and the external wall, there are muscle fibers, often branched, especially at the ends. The ventral projections of the limiting membrane into the ridges of the disc form two sides of long triangular prisms, which extend longitudinally and transversely above the musculature of the disc. One face of these prisms is dorsal and the opposite angle is extends ventrad, increasing the size and prominence of the ridges which separate the disc into fossetes.

Alimentary tract. The mouth funnel is a cup shaped muscular structure (Fig. 59), which functions as an organ of adhesion. There is no oral sucker. This anterior sucker or mouth funnel is 0.08 to 0.1 mm in daimeter, sub-terminal in position. There is no prepharynx, the mouth funnel opens directly into the lumen of the pharynx. The latter is a spherical muscular organ 0.09 to 0.1 mm in diameter. It is followed by a very short esophagus, a specialized portion of the alimentary tract. In the anterior part it has a cuticular lining and in the posterior part a lining of flattened epithelial cells. The esophagus passes over posteriorly into the intestine, an elongated sac or tube extending on the dorsal side of the body 0.1 to 0.2 mm posterior to the caudal edge of the testis. It varies but slightly in caliber, averaging about 0.075 mm in diameter. The wall consists of a fibro-muscular layer upon which rests a layer of columnar epithelial cells. The large, deeply staining nuclei of the epithelial cells lie in the basal part, while many delicate, elongate processes extend out into

the lumen of the canal.

Male Reproductive Organs. The testis is large, single, median, situated 0.25 to 0.35 mm from the posterior end of the forebody, and occupies the anterior third of the posterior half of the region of the adhesive disc. It is almost spherical and measures 0.25 to 0.35 mm in diameter. Cells of various sizes and with the chromatic material in various stages of division as well as mature spermatozoa are to be seen in sections. The sperm duct arises at the anterior part of the testis and turns to the left, entering the side of a long, much coiled seminal vesicle (Fig. 55). This vesicle is a large tube, 0.1 to 0.175 mm in diameter, extending from the region of the testis to the cirrus sac. It is coiled eight to sixteen times and in all the mature specimens is filled with spermatozoa. Terminally it is constricted into a small tube and enters the large cirrus sac. This structure is 0.145 to 0.2 mm wide and 0.2 to 0.25 mm long, has a strong muscular wall, and is pyriform in shape the smaller end opening anteriorly at the genital pore. Inside the cirrus sac there is a dilated, curved portion of the duct which has muscular walls and is lined with epithelial cells. Surrounding the duct and filling the cirrus sac there are large unicellular prostate glands. These are pyriform and average twenty six micra long and seventeen micra wide. The cirrus was observed in the extruded condition.

Female Reproductive Organs. The ovary is a small organ triangularly ovoid in shape, averaging 0.18 mm in length, 0.1

mm in width and 0.05 mm in thickness. It is located at the right of the median line, about midway between the cephalic and caudal ends of the forebody. In well extended specimens it is nearer the posterior end and in contracted ones nearer the anterior end. The oviduct arises at the posterior margin of the ovary and passes posteriorly, receives a short duct from a vitelline receptacle, and then expands into two or three irregular enlargements. Mehlis gland is present, the nuclei lying in the parenchyma around the ootype. The uterus passes posteriad on the lateral side of the collecting duct of the excretory system as far as the caudal end of the testis where it turns to the median line. Here it passes ventrad and anteriad beneath the testis; in front of the testis it turns dorsad and toward the ovary, but just before reaching the ovary it turns about and crosses to the opposite side of the body and passes with little deviation to the genital pore (Fig.55). Eggs were present at various places in the course of the uterus, and when the worms were placed in tap water, the eggs near the pore were extruded. The eggs are few in number, not more than six were present in any specimen. In size they vary from 0.071 to 0.083 mm in width and from 0.137 to 0.145 mm in length. The average of twenty five was 0.141 by 0.075 mm. The vitellaria are arranged along the sides of the forebody, extending from the posterior end to the level of the cirrus sac. The follicles are more numerous and closer together at the posterior region, gradually becoming fewer in the anterior part of the vitelline zone. They lie just above the limiting membrane which forms the dorsal boundary of the musculature of

the adhesive disc, and number up to forty on each side. In size they vary from ten to forty micra in diameter. In some specimens they appear to arranged in a double row on each side with the follicles placed alternately, but there is common and wide variation from this condition. Vitelline collecting ducts extend along the median face of the vitellaria and at the level of the cotyre pass mediad where they unite to form the vitelline receptacle.

The common genital pore is in the median line, on the ventral side of the forebody, above the point of attachment of the adhesive disc. There is no genital atrium, the two ducts open to the exterior separately, the opening of the cirrus sac is on the right and that of the metraterm on the left.

Excretory System. (Fig. 53) Most of the observations on this system were made on living specimens. As the water evaporated from under the coverglass the worm was flattened, and the larger excretory tubules could be easily followed. The pore is dorsal, at the posterior end of the forebody. There is a single excretory vesicle, situated between the large flask like ends of the collecting ducts and the pore. In the pulsations of this organ, the anterior ventral part contracted and the constriction passes posteriad and dorsad, expelling the fluid thru the pore. Two collecting ducts extend cephalad from the excretory vesicle, one on either side of the forebody, median to the vitellaria. Just posterior to the pharynx each duct divides, sending a branch cephalad on the lateral side of the pharynx and anterior sucker and a second branch turns caudad.

This caudal branch subdivides into a branch extending to the region of the genital pore, and a longer, larger branch which passes posteriorly to the region of the testis and receives many smaller side branches. Cross sections show the collecting ducts to be dorsal in position.

Sensory Structures. There is a dorsal nerve commissure crossing the anterior part of the pharynx, and lateral nerves were traced running cephalad and caudad from it. In about one half of the specimens a pair of black pigment spots were present on the dorsal commissure. These "eyes" are dorsad of the lateral walls of the pharynx (Fig. 60). No lens is present.

At the ends of the cross partitions of the adhesive disc are the"marginal organs",(Randkörper of Looss). These structures occur on the ventral side in the angles where the transverse ridges meet the musculature of the margin of the disc. Leading dorsad from the exterior there is a narrow canal, which is surrounded by strong muscles, and this terminates in a large spherical cavity. The cavity is lined with cuticula, continuous with that of the external surface of the body. In some cases the cavity was empty, in others it contained a granular or alveolar fluid like substance. At the dorsal part of the bulb there are fibers, probably muscular, passing to the limiting membrane which forms the dorsal wall of the musculature of the disc. Also in the region around the dorsal part of these organs there are many nuclei of parenchymatous tissue. In the study of the living worms it was noted that these organs were everted and retracted as the animal moved. They were moved rapidly and when extended, resembled everted

membranous sacs. The rapid, correlated and accurate movement would suggest a good nerve supply, altho no nerve cells or fibers were demonstrated. Nickerson (1900) describing these organs in Cotylogaster, described a bundle of nerve fibers entering the bulb at its basal end, and a cluster of bipolar nerve cells lying upon the side of the bulb against which the tube is coiled back when retracted. He states that the presence of the bipolar cells establishes the senrory character of these organs, and believes them to be both sensory and glandular in function.

Comparisons. This is the third aspidocotylean described from turtles, the two previously reported forms are Cotylaspis lenoiri Poirier 1886, and Lophotaspis vallei Stossich 1899, both African forms. Poirier described C. lenoiri from the intestine of Tetrathyra vaillanti of Senegal, and Looss (1902) reports it as occurring in Trionyx notilica of the Nile. Lophotaspis vallei is parasitic in the stomach of Thalassochelys corticata of Egypt. C. cokeri is very different from Lophotaspis, but shows considerable resemblance to C. lenoiri. A comparison of the description of C. lenoiri with specimens of C. insignis and C. cokeri shows decided differences in the sizes and shapes of the worms, shape and size of the adhesive disc, number of alveoli and marginal organs, size of ovary and testis, size of cirrus sac and size of eggs. The three forms agree in essential morphological features and fit the diagnosis of the genus Cotylaspis as given by Leidy.

Classification. The last classification of the Aspidogastridae was made by Nickerson (1902). Since additions and changes have been made in recent years, further revision seems advisable. The present arrangement is largely based on the work of Nickerson and brings the classification to date. Present information supports the validity of the following genera.

I. Aspidogaster von Baer 1827.

Type species, A. conchicola von Baer.

Oval adhesive disc, four rows of alveoli, margianl organs present, mouth subterminal, no oral sucker, one testis. This genus contains A. conchicola, which infests the pericardium and renal organs of various species of Unionidae in Europe and North America. It is also found in Gastropods and in the immature condition in the intestine of Unionidae. Other species of this genus are A. limacoides Diesing 1834 from the intestine of a fish (Leuciscus) in Europe, a form which Stafford (1896) and Kofoid (1899) suspect of being identical with A. conchicola. The species A. macdonaldi was placed in this genus by Monticelli (1892) and removed to Lophotaspis by Looss (1902). Linton (1905) described A. ringens from the intestine of Micropogon undulatus and Trachinotus carolinus at Beaufort, N. Carolina. Mac Callum and Mac Callum (1913) gave a more complete description of A. ringens, and described A. kemostoma n. sp. both species from the intestine of Trachinotus carolinus.

II. Cotylaspis Leidy 1857.

Type species, C. insignis Leidy.

Oval adhesive disc, three rows of alveoli, marginal

organs present, mouth subterminal, no oral sucker, one testis. This genus contains the species C. insignus, C. lenoiri, and C. cokeri. C. lenoiri was described by Poirier (1886) as a species of Aspidogaster. Monticelli (1892) created a new genus Platyaspis to contain Poirier's species, evidently overlooking the similarity between it and the form reported by Leidy. He declined to accept the genus Cotylaspis, suggesting that C. insignis was a species of Aspidogaster. Braun (1893) ascribed the species to Aspidogaster. Kofoid (1899) established the validity of Leidy's genus but contended that the genus Platyaspis should be retained for Poirier's species. Nickerson (1902) argues that the differences between the African and American form are not of generic importance and suppressed the genus Platyaspis, making Aspidogaster lenoiri Poirier, and Platyaspis lenoiri (Poir. 1886) Monticelli 1892 synonomous with Cotylaspis lenoiri Poir. The genus Cotylaspis contains the species C. insignis Leidy, occurring ectoparasitically in the mantle cavity of Unionidae in North America; C. lenoiri Poirier, from the intestine of the turtle Tetrathyra vaillanti of Senegal and Egypt; and C. cokeri Barker and Parsons, from the intestine of the turtle Malacoclemmys leseurii from North America.

III. Macraspis Olsson 1868

Type species, M. elegans Olsson.

This genus has a single row of confluent acetabula in the adhesive organ, marginal organs present, mouth terminal, one testis. The single species is parasitic in the gall bladder of Chimaera monstrosa, a fish from the coast of Europe.

IV. Stichocotyle Cunnungham 1884.

Type species, S. nephropis Cunningham.

There is a single row of more or less distinct acetabula, marginal organs lacking, mouth sub-terminal, oral sucker absent, two testes. Cunningham's original description was of the larva and Monticelli (1892) declined to recognize its generic importance thinking it might be a form of Macraspis. Odhner (1898) by discovering the adult and tracing the life history, established the genus. Adults live in the bile ducts of the liver of rays; larvae occur encysted in the wall of the intestine of the larger marine Crustacea. Cunningham described it from the Norwegian lobster, Nephrops, and Nickerson (1895) reported it from the American lobster, Homarus americanus.

V. Cotylogaster Monticelli 1892.

Type species, C. michaelis Monticelli.

Adhesive disc with three rows of alveoli, marginal organs present, mouth terminal, oral sucker present, two testes. There are two species. C. michaelis occurs in the intestine of Cantharus vulgarus, a European fish. C. occidentalis Nickerson (1899) occurs in the intestine of Aplodinotus grunniens of North America.

VI. Lophotaspis Looss 1902.

Type species, L. vallei (stossich) 1899.

Adhesive organ with four rows of alveoli; marginal organs present at all the intersections of the ridges of the adhesive disc; cirrus absent. Looss (1901) reported L. adhaerens as a worm belonging to a new genus of Aspidogastridae, but was not aware that Stossich (1899) had described the same form as Aspidogaster vallei. Looss (1902) described and figured

the form as Lophotaspis vallei. In the same paper Looss compared A. macdonaldi with L. vallei and placed the former species in the genus Lophotaspis. This trematode was reported by Macdonald in 1878 but not named by him, and Monticelli (1893) named the form as a species of Aspidogaster. Nickerson (1902) declared it to be an aspidogastrid, but different from all other known aspidogastrids, and predicted that a new genus would have to be erected for it when its structure was better known. Macdonald reported 180 extensile structures, like the tentacles of a snail, occurring at the margins and intersections of the ridges of the adhesive disc. Nothing is known of the internal structure. Looss in placing the form in the genus Lophotaspis states, "Mit ihrer tentakeltragenden Bauchschiebe bildet die Art aber ganz zweifellos einen fremden Eindringling in der Gattung Aspidogaster, in dessen typischen Art jedenfalls solche Tentakel nicht besitzt. Gerade diesen auffallenden Character aber teilt sie mit Lophotaspis; ich bin geneigt, A. macdonaldi Monticelli, trotsdem bei ihm die Genitalöffnung weiter rückwärts liegt als bei Lophotaspis vallei, aus dem Genus Aspidogaster herauszunehmen und zu lophotaspis zu stellen."

## V. Paramphistomidae

The genus Amphistoma was created by Rudolphi (1801), and Stiles and Hassall (1908) state, "Rud. deliberately renamed a previously validly named genus, namely Strigea Abildgaard, 1790, referring clearly to this fact both in 1801a, 50-51, and 1802b, 92. He makes but one combination (Amphist. subclavatum), but since Amphist. is clearly a new name proposed for an older one (Strigea), which Rud. changed on the alleged ground that it was inappropriate, Amphist. should be suppressed in favor of Strigea and take the same species as type."

The family Amphistomidae was proposed by E. Blanchard (1847) to contain the genus Amphistoma, and successive writers added other genera to the family. Fischoeder (1903) says, " In Bezug auf den Namen Amphistomum will ich jedoch, wie schon gesehen (1901), nochmals darauf hinweisen, dass der Name Amphistoma von Rudolphi (1801) alz neue Bezeichnung für die Gattung Strigea Abildg. 1790 eingeführt worden ist. Der Name Amphistoma kommt daher nach dem Prioritätsgesetz als Synonym zu Strigea in Fortfall. Die ursprüngliche einzige und also auch typische Art der Gattung Strigea Abildg. 1790 (= Amphistoma Rud. 1801) war Planaria strigis Goeze 1782 = Amphistoma macrocephalum Rud. 1809 = Holostomum macrocephalum Nitsch. 1819). Wenn daher der Name Strigea wieder zu Geltung wieder gebracht werden soll, so darf er nur für die heutige Gattung Holostomum weitergeführt werden, während die heutige Gattung Amphistomum einen anderen Namen erhalten muss. Ich habe( in: Zool. Anz. 1900, V. 24, p. 367) den Namen Paramphistomum vorgeschlagen und, die Eintheilung nach dem Fehlen oder Vorhandensein der Pharyngealtaschen

beibehaltend, in der Fam. Paramphistomidae Fischdr. (= Amphistomidae Montic. 1888) die Unterfamilien Paramphistominae und Cladorchinae Fischdr. unterschieden. In diesen beiden Unterfamilien lassen sich die bekannten Formen unterbringen."

The paramphistomes of mammals have received extensive study at the hands of Fischoeder (1903) and Stiles and Goldberger (1910); and a number of species are known.

No work was done on paramphistomes of fish between that of Diesing (1836) and Mac Callum (1905). Daday (1907) described two species of Diplodiscus, two species of a new genus Microrchis, three species of a new genus Pseudocladorchis, and added Amphistoma oxycephalus and two new species to the genus Cladorchis. He included a section on the anatomy and histology of the forms.

Four species of Diplodiscus have been reported from frogs; D. subclavatus from the frogs of Europe, D. temperatus from North America, and D. megalochrus and D. microchrus from Australian frogs.

Information concerning paramphistomes of reptiles is very scanty. Braun (1901) lists three species from turtles, Amphistoma grande Diesing, A. sclerororum Creplin and A. sp. Bellingham. Bellingham (1844) lists A. sp from the intestine of Chelonia imbricata but gives no description. Braun is inclined to discredit this species. In his (1901) paper he supplements the description of Creplin (1844) by a brief report of the single specimen of A. sclerororum from the museum at Greifswald, but the worm was sexually immature and consequently the observations limited. A. grande Diesing was collected by Natterer from the

intestine of five species of turtles in Brazil, but the description of Diesing is confined to the external appearance and the material may have comprised more than one species. One other species is known from turtles, a form described by Looss (1902) as A. spinulosum from the intestine of Chelone mydas. The description of Looss is very complete but because of the scarcity of known species and our limited knowledge of the group, at that time he refrained from any attempt at classification. He stated that the species is probably closely related to A. scleroporum and A. grande. In addition to the description of the species, he discusses the question of the oral sucker and the pharynx of the group and compiling evidence from comparative anatomy and embryology, he argues that the anterior sucker of the amphistomes is homologous to the oral sucker of the distomes. In this paper Looss described the muscular thickening at the caudal end of the esophagus as a pharynx and described a peristaltic contraction of the organ from the anterior to the posterior end. Looss (1896) says the esophageal thickening of Gastrodiscus is not a true muscular pharynx. Odhner (1911) concerning this structure says, "Ich verwende diese Bezeichnung, weil es mir doch nicht so ganz sicher erscheint, dass es sich hier um ein dem gewöhnlichen Distomenpharynx homologes Organ handelt. Auch wenn es so wäre, könnte übrigens der ziemlich verschiedene Bau einen besondern Namen rechtfertigen; der Oesophagus müsste aber dann konsequenterweise als Präpharynx bezeichnet werden." In his later paper Looss (1912) refers to this organ as an esophageal bulb. The arrangement of the muscle fibers in concentric lamellae and the function of the organ, acting as a sphincter

instead of a dilating pumping organ, argue against its homology with the pharynx of the distomes. In Zygocotyle ceratosa n.sp. however, instead of concentric lamellae of muscles, the fibers at the sides of the lumen are placed radially. A thickening of the musculature of the esophagus is described for Gastrodiscus, Homalogaster, Diplodiscus, Microrchis, Chiorchis, Schizamphistoma, Alassostoma and Zygocotyle. The writer regards the tube leading from the oral sucker to the intestine as the esophagus and the muscular thickening of the wall of the esophagus as an esophageal bulb.

Looss (1912) reinvestigated the species Amphistoma scleroporum and described the structure of the form in detail. Discussing the taxonomy of the species he says," Die Frage nach den Verwandtschaftlichen Beziehungen des Amph. scleroporum ist insofern leicht beantwortet, als seine enge Verwandschaft zu A. spinulosum, auf die ich schon früher vermutungsweise hinwies (1902b, p. 437) jetzt offen zutage tritt. Ich würde nicht zögern, beide Arten in dieselbe Gattung einzureihen, wenn nicht gewisse, wenn auch kleine Differenzen im anatomischen Baue existierten die meiner Auffassung nach innerhalb von wirklich natürlichen Gattungen nicht vorkommen. Diese Differenzen bestehen, 1. in dem Fehlen des vor dem Mundsaugnapfe gelegenden starken Sphincters von A. scleroporum bei A. spinulosum; 2) der Reduktion der Saugnapftaschen, die bei A. spinulosum deutlich, bei A. scleroporum nicht nach aussen hervortreten; 3. dem Fehlen der kleinen Seitenzweige an den vordersten Enden der Blasenschenkel von A. scleroporum bei A. spinulosum; 4. in dem etwas abweichenden Bau der Dotterstöcke ( bei A. scleroporum in der

Mitte fast zusammenstossend und ohne eigentliche quere Dottergänge, bei A. spinulosum rein seitlich mit langen queren Dottergängen); 5. in dem etwas verschiedenen Verhalten der Lymphschläuche (ungemein reiche Verzweigung im Umkreise der Saugnäpfe bei A. scleroporum, kaum angedeutete Verzweigung bei A. spinulosum). Bin ich demnach auf Grund dieser Unterschiede auch überzeugt, dass in den beiden Arten Repräsentanten je eines besondern Genus vorliegen, so genügt für meinen gegenwärtigen Zweck doch die formelle Aufstellung der Gattung Schizamphistomum für A. scleroporum, in die ich A. spinulosum vorläufig provisorisch einbeziehe. Als die wesentlichen Charaktere dieser Gattung oder der Unterfamilie, zu der sie sich früher oder später auswachsen wird, betrachte ich den Aufbau der Excretionsblase aus 2 sehr langen, bis ins Kopfende einfachen, unter sich nicht verbundenen Schenkeln und den Aufbau des Lymphgefässsystemes aus jederseits 3 in der Umgebung der Saugnäpfe verästelten Schläuchen."

He might well have added to his list of differences that in S. spinulosum there is a single loop of the excretory vesicle wound dorsally over the cecum of each side while in S. scleroporum there are eight loops winding irregularly around the cecum of each side. In the same article, p.355 speaking of the excretory system in paramphistomes of mammals he says this system is situated deeply in the body and is "innerhalb grösserer Gruppen stabilen und konservativen Organsystems,". In a former paper Looss (1902:827) he says, "Zwischen den Species einer natürlichen Gattung bestehen anatomische Unterschiede nicht; die Speciescharaktere werden dargestellt allein durch Differenzen in der Grösse des Körpers und der einzelnen Organe, Hand in Hand

mit denen leichte Veränderungen ihrer Form, ihrer Lage und wenn sie reicher gegliedert oder in eine Anzahl von Theilstücken zerfallen sind, Aenderungen in der Zahl der Glieder resp. der Theilstücke gehen können." Instead of justifying the inclusion of the two species in a single genus, the argument of Looss appears to show clearly that S. sclerosporum and S. spinulosum are not members of the same genus; and while they undoubtedly belong to closely related genera, the anatomical differences seem too great to permit their continuance in a single genus.

The single paramphistome reported from snakes was described by Cohn (1903) as Amphistomum dolichocotyle, and in his (1904) classification of the Diplodiscinae placed in the genus Catadiscus. It is from the intestine of Herpetodryas fuscus.

Stiles and Goldberger (1910) proposed a new classification of the Paramphistomidae. They propose a new superfamily Paramphistomoidea . They removed Gastrodiscus Leuck. and Homalogaster Poir. from Fischoeder's subfamily Cladorchinae and created a new family Gastrodiscidae to contain these genera. They created a new family Gastrothylacidae to contain the genera Gastrothylax, Wellmanius, Carmyerius and Fischoederius. These with the family Paramphistomidae comprise the three families in the superfamily Paramphistomoidea. These authors created a new subfamily Stephanopharynginae to contain the genus Stephanopharynx, and add the new genus Cotylophoron to the subfamily Paramphistominae. They recognize the subfamily Diplodiscinae Cohn and list the four subfamilies Paramphistominae, Cladorchinae, Diplodiscinae and Stephanopharynginae in the

family Paramphistomidae. They place Balanorchis in the subfamily Cladorchinae notwithstanding Fischoeder's statement that such an arrangement could not be considered.

Braun, reviewing the article in the Zoologisches Zentralblatt, 18: 705, objects to the rank superfamily for the paramphistomes, and says placing them on an equality of rank with the Fascioloidea is not justifiable.

The work of Stiles and Goldberger received a harsh criticism at the hands of Odhner (1911) who states, "Dies alles zeigt nun evident, wie wenig Verständnis die betreffenden Autoren für die moderne natürliche Digenensystematik haben.... Mir scheint nun diese "Argumentation" ebenso wie viel andres (die neue topographische Terminologie) in derselben Arbeit sehr "unwise" zu sein,..... die Amphistomen entsprechen im systematischen Range einer einzelnen Distomenfamilie und nicht, wie Stiles and geglaubt haben, der Summe sämtlicher dieser Familien."

Looss (1912) gives a severe and critical review of the paper, " Die Charakterisierung der Arten, Gattungen usw. baut sich auf, einerseits auf eine pedantisch ins einzelne gehende Analyse und Beschreibung der Körperform und der Topographie von Darm und Genitalapparat, andererseits auf eine konsequente Ignorierung der beiden Tatsachen, dass die Tiere, als Organismen, innerhalb gewisser Grenzen natürlich variieren, und dass Körperform sowohl wie Topographie der Organe mit dem Wachstum gesetzmässige, mit der Kontraktion a priori nicht bestimmbare Veränderungen erleiden. Der Aufbau von Lymph- und Excretionsapparat bleibt völlig unberücksichtigt. Dass die Amphistomen ein "Lymphgefässsystem" überhaupt besitzen, scheint den Autoren

unbekannt zu sein."

The only paramphistomes previously known from North America are Amphistoma grande, reported by Leidy (1888) from the intestine of the terrapin; two specimens from the small intestine of the muskrat which"appear to belong to Amphistoma subtriquetrum", Leidy (1888); Diplodiscus temperatus Stafford, long considered as identical with D. subclavatus Dies.; and Wardius zibethicus Barker and East (1915), from the cecum of Fiber zibethicus. The reports of Leidy contain no description except the length of the worms. Barker and East suspect that the specimens from the muskrat belong to the new genus and species Wardius zibethicus; and it is not unlikely that the specimens from the terrapin are specifically identical with those described in this paper as Allassostoma magnum n.g. n.sp. Neither the descriptions of Stafford or Barker and East contain complete anatomical information. Stafford distinguished between the lymph and excretory systems. Barker and East make no mention of the lymph system. These authors state," Oral sucker absent"; and describe the anterior sucker as the pharynx, in spite of the arguments of Pratt (1900), Looss (1902) and Stiles and Goldberger (1910) that the anterior sucker of the amphistomes is homologous with the oral sucker of the distomes.

The material of this family available for the present study consisted of representatives of two species from North American turtles, and another species from the duck, Anas platyrhynchos. A study of the literature showed that these forms could not be included in any previously described genera.

The two species from turtles are included in the new genus Alassostoma and a discussion and comparison of the genus follows the descriptions of the species.

Alassostoma magnum n. sp.

The material of this species consists of one worm from Pseudemys troosti from Havana, Illinois; one from P. elegans from the same locality; two from P. elegans from Chicago, Ill: and three specimens from an unknown turtle from Marshall, Missouri. The first four specimens were collected by the writer from the large intestine near its juncture with the small intestine, and the material from Marshall, Mo. bears the label "From cloaca of turtle".

These worms are 10 to 12 mm in length, 3 to 5 mm in breadth, and 1.5 to 2 mm in thickness. One specimen, studied in the living condition, measured 18 mm in length when fully extended; preserved it is 11 mm long, 3.8 mm wide and 2 mm thick. One specimen 10 mm long and 3 mm wide is not sexually mature.

In the living state the specimens are clear, hyaline, with the digestive ceca visible as brown lines. Their movements were very slow. In shape the worms (Fig. 31) are more or less oval, with the acetabulum forming a slight caudal projection. The acetabulum is slightly sub-terminal, circular or ovoid, usually wider near the anterior than the posterior end. The opening is necessarily relatively narrower than the sucker itself, in one case the opening is merely a slit, 1.4 mm long, 0.38 mm wide near the anterior end and posteriorly tapering to a point. In the largest specimens the acetabulum is 2.5 mm long, by 2 mm wide, and in the smallest it is 2 mm by 2 mm.

The cuticular covering of the body is unarmed, and measures 10 to 12 micra in thickness. It is turned in at the openings of the excretory and reproductive systems and lines the digestive tract to the bifurcation. The dermo-muscular wall has the circular, longitudinal and oblique layers well developed, and inside the oblique layer there are additional sets of longitudinal fibers (Fig. 36). Dorso-ventral fibers are scanty or lacking, and the parenchyma of the body is very loose and vacuolated (Fig. 62).

Alimentary tract. The oral sucker is terminal, spherical to ovoid in shape, usually longer in the antero-posterior axis, and somewhat wider anteriorly than posteriorly. It is deeply set in the parenchyma of the body and measures 0.9 to 1.35 mm in length and 0.6 to 0.9 mm in width. Radial fibers pass from the external limiting membrane to the cuticula lining the sucker; in a cross section thru the sucker (Fig. 37), the inside two thirds of the outer half is a nuclear zone and all the nuclei are collected in this area. Half way between the nuclear zone and the lumen there is a narrow band of circular fibers. The oral evaginations arise at the caudal end of the oral sucker by two separate openings, one on either side, and extend dorsad and caudad. They are 0.35 to 0.6 mm long, flattened dorso-ventrally, 0.15 to 0.2 mm in width. These saca are lined with cuticula, and their wall is continuous with that of the oral sucker. Externally there is a layer of longitudinal fibers and inside this sets of annular fibers (Fig. 38). Oblique and radial fibers are occasionally seen but are very scanty.

The esophagus is 0.6 to 1.3 mm in length, it is lined

with cuticula and the wall contains external longitudinal and internal annular fibers. At the caudal end of the esophagus, just anterior to the bifurcation of the alimentary tract, there is a prominent esophageal bulb. It varies from 0.35 to 0.95 mm in length and from 0.37 to 0.5 mm in width; and is composed of a thickening of the annular fibers of the wall of the esophagus. A cross section is represented in Fig. 66 and shows the eighteen concentric lamellae of muscles. No nuclei are present in these annular muscles. Both the oral evaginations and the esophagus are surrounded by clusters of deeply staining cells. Looss (1896) described similar cells in Gastrodiscus and believed they secrete the lining of the esophagus. The ceca are flattened laterally, and are of very unequal caliber, lateral evaginations occur on opposite sides at the same level, recalling the condition in some of the Turbellaria. The diverticula extend almost to the acetabulum, about 0.37 mm intervening. They have a muscular coat similar to that of the esophagus, and the epithelial lining has masses of cilia like processes extending into the canal (Fig. 64).

Male Reproductive Organs. The testes are slightly lobed, oval, longer in the transverse diameter, and vary in measurement from 0.27 by 0.35 mm to 0. 45 by 0.9 mm. They are situated one behind the other or in contracted specimens on opposite sides of the median line. They are approximately the same size in any one specimen and are separated by about the length of one of the testes. The vasa efferentia arise from the dorsal anterior margins, the duct from the posterior testis on the left and the duct from the anterior testis on the right side

of the body. They pass dorsad and cephalad, and 0.4 to 0.5 mm caudad of the bifurcation of the digestive tract they unite to form a single tube. This expands to form a much coiled seminal vesicle, which near the pore passes into a small, poorly developed cirrus sac. In sectioned individuals the seminal vesicle was filled with spermatozoa. In one specimen the coils of the vesicle extend thru twenty cross sections, each fifteen micra in thickness, and the tube is so coiled that in sections of the worm there are ten or fifteen sections of the vesicle. In another individual cut in frontal sections the seminal vesicle extends thru 0.57 mm. The prostate gland is enclosed by the cirrus sac. The sac is approximately 0.37 mm long and 0.185 mm in diameter. It is dorsal, on the right side of the body and the terminal end of the uterus is ventral, on the left side of the body.

<u>Female Reproductive Organs.</u> The ovary is spherical or oval, 0.275 to 0.35 mm in length and 0.33 to 0.57 mm in width, in or near the median line, about the width of the caudal testis behind it. The oviduct is very small and arises from the dorsal margin of the ovary (Fig. 65). After a coil posteriad Laurer's canal is given off and passes in a winding course to the dorsal surface. There is no receptaculum seminis. Just after the origin of Laurer's canal, the oviduct passes into the Mehlis' gland, where the vitelline duct is received. There is no vitelline receptacle in either of the sectioned worms; but the right and left ducts are very large. They meet in the median line, posterior and ventral to the Mehlis' gland, and a short duct passes to the ootype. The uterus coils anteriad,

either between or around the testes and enters the hermaphroditic duct to the genital pore.

The genital pore is in the median line, ventral to the esophageal bulb, and there is a small genital sinus. The cirrus sac and metraterm[al] portion of the uterus open into a common hermaphroditic duct (Fig. 63), which opens to the exterior at the apex of a genital papilla.

The vitellaria consist of small irregularly shaped follicles, lying almost entirely in the ventral half of the body, and extending from the region of the cephalic testis to the caudal ends of the ceca. Anteriorly they are extracecal, but posteriorly they extend into the intracecal areas; at the ends of the ceca approximately one half of the follicles are between the diverticula.

Three eggs are present in one specimen. They measure 0.1 by 0.13 mm.

The Lymph System. This system consists of three canals passing longitudinally on either side of the body, one lateral and two medial of each cecum. Of the median pair, one is dorsal and the other ventral (Fig. 61). These canals are not straight, but wind about and give off branches at various points. These branches subdivide in turn, and at the ends the main trunks break up into numerous smaller branches so that the entire body is penetrated by ramifications of this system. The ceca, the genital organs, and the suckers are especially well supplied with lymph sinuses.

Excretory System. The excretory pore is in the median line, on the dorsal surface, and the median terminal vesicle

extends internally and anteriorly. It gives off a branch to either side and these branches of the collecting vesicle pass anteriad, winding about the cecum of either side in many loops or coils. In sections (Fig. 63) the tube may appear on either side, above or below the cecum; in a single section it may be cut in two or three places or a loop may pass half to two thirds of the way around the cecum. No connections between the collecting ducts of the two sides were seen. The collecting vesicles were traced to the region of the oral sucker.

Alassostoma parvum n. sp.

Three individuals of this species were collected from the cloaca of a single specimen of Chelydra serpentina from Urbana, Ill. One was retained as an alcoholic specimen, one was stained and mounted as a toto preparation, and the third was cut into cross sections.

The worms (Fig. 68) are thick with almost parallel sides, rounded at the posterior end and tapering slightly anteriorly. Just anterior to the acetabulum the body narrows slightly and then widens posteriorly due to the presence of two lateral prominences or evaginations, one on either side at the level of the anterior part of the acetabulum. The worms are 2.8 to 3 mm long and 0.78 to 0.8 mm wide, the points of greatest width are at the level of the testes and thru the posterior lateral prominences. The sectioned worm is 0.8 mm in width and 0.54 mm in thickness. The acetabulum is sub-terminal, oval, 0.8 mm in length and 0.7 mm in width in the toto preparation. The inside measurements of the same sucker are 0.56 mm in length by 0.4 mm in width and the opening is 0.45 mm in length and 0.21 mm in greatest width.

Alimentary Tract. The oral sucker is terminal, ovoid, 0.46 mm long by 0.37 mm wide and in the sectioned worm the oral sucker is 0.32 mm in depth. In the mounted specimen the sucker is widest posteriorly, and from the posterior dorsal part on either side there is an oral evagination. These arise separately, and are 0.065 mm long. Among the fibers of the oral sucker there are many nuclei, they are situated in the peripheral half of the sucker and are confined to the central two thirds of the

external half. There are also among the muscle fibers gland cells with ducts to the lumen of the sucker. The esophagus is somewhat coiled but extends thru 0.2 mm and is surrounded by large deeply staining gland cells (Fig. 70). The posterior part is thickened by an enlargement of the annular muscles of the wall and forms the esophageal bulb. This structure comprises twelve concentric rings or lamellae of muscles. It is 0.? mm long by 0.14 mm wide in the toto specimen and 0.114 mm in depth in the sectioned individual. The diverticula extend posteriad almost to the cephalic margin of the acetabulum. In sections they are oval, flattened laterally. In the intestine of the sectioned worm there are masses of small nuclei, possibly from the epithelial lining of the cloaca of the host.

Male Reproductive Organs. The testes are oval, in the toto specimen they are 0.17 mm long by 0.17 mm wide, and in the sectioned worm the testes are 0.17 mm wide by 0.29 mm thick. They are situated one in front of the other, in the median line, and in the ventral part of the body. They are close together, separated only by a thin fibrous sheet. The vasa efferentia arise at the dorsal margins of the testes; the duct from the caudal testis passes anteriad and at the anterior dorsal region of the cephalic testis unites with the duct from this testis and the vasdeferens immediately expands into a long much coiled seminal vesicle which passes anteriad and into the cirrus sac (fig. 71). Inside the cirrus sac the tube continues in many large coils. The terminal part is surrounded by the cells of the prostate gland and terminates in a short hermaphroditic duct which opens to the surface at the apex of the genital papilla

(Fig. 69).

Female Reproductive Organs. The ovary is oval, in the toto specimen it is 0.098 mm long and 0.098 mm wide, and in the sectioned worm it is 0.095 mm wide and 0.134 mm thick. It is median in position, situated midway between anterior and posterior ends. The oviduct arises at the dorsal posterior margin and passes dorsad and posteriad into the Mehlis' gland. This gland is large and well developed. Here Laurer's canal is given off and passes in short coils to the dorsal surface. Just after the origin of Laurer's canal a short common vitelline duct opens into the ootype and the oviduct passes ventral. It expands to form the anterior part of the uterus, turns anteriad, and is filled with masses of spermatozoa. The expanded section of the uterus extends anteriad half the distance to the caudal testis and then the tube contracts, passes dorsad and in a winding course over the testes. Anterior to the testes it turns ventrad and enters the hermaphroditic duct on the posterior ventral side. The vitellaria extend from the region of the testes to the caudal ends of the digestive ceca, and consist of scattered lobes, mostly ventral in position. Anteriorly they are extracecal but behind the ovary they are intra- as well as extracecal.

No eggs were present in any of the specimens.

The genital pore is in the mid-ventral line, just posterior to the bifurcation of the alimentary tract. There is a genital sinus but no genital sucker.

Lymph System. The lymph system is similar to the same system as described for Alassostoma magnum, it consists of the three longitudinal canals on either side of the body, one canal lateral to each cecum, and a pair, one dorsal and the other ventral mesal to the diverticulum of either side. The secondary branchings could not be traced in the toto preparation, but lymph sinuses are present in sections in all parts of the body, and those around the acetabulum are shown in Fig. 73.

Excretory System. The excretory pore is median, dorsal, at the level of the cephalic margin of the acetabulum. A short median vesicle passes ventrad and anteriad and divides into two collecting vesicles as in A. magnum. These pass ventrad and posteriad looping around the caudal ends of the diverticula, and then pass anteriad winding around the ceca in many irregular coils so that in sections they appear lateral, mesal, ventral or dorsal to the intestine, often the tube is cut two or three times in the same section, or a single section may show a coil encircling the cecum for half or more of its circumference (Fig. 72). Anterior to the bifurcation of the ceca the ducts continue in the lateral areas of the body and can be traced almost to the oral sucker.

Comparisons. Comparing the species A. magnum and A. parvum with descriptions in the literature, they agree most closely with Schizamphistoma sclerororum and S. spinulosum Looss. Mention has previously been made of the anatomical differences existing between these species and a statement ventured that such wide and fundamental differences should not be present in a natural genus. Alassostoma magnum agrees with S. sclerororum in

general appearance and size, in type of excretory and lymph systems, character of vitellaria, and in general type of reproductive and alimentary organs; but A. magnum has large oral evaginations, which pockets are reduced and do not extend outside the sucker in S. scleroporum, and A. magnum lacks the preoral sphincter which is present in S. scleroporum. In A. magnum the uterus and cirrus sac open to the surface thru a common hermaphroditic duct; in S. scleroporum they open separately. Looss (1899: 551) says one of the most important of generic characters is the character of the copulatory organs. In A. magnum the reproductive organs are smaller, the testes are farther posterior and the ovary is situated one fourth to one third of the body length from the posterior end instead of at the level of the anterior margin of the acetabulum as is the case in S. scleroporum. In S. scleroporum the testes and ovary are widely separated and in A. magnum they are comparatively close together. These differences appear to be of sufficient importance to exclude the American species from the genus Schizamphistoma.

A. magnum agrees with S. spinulosum in the presence of oral evaginations, lack of preoral sphincter; but differ from it in the manner of coiling of the paired excretory collecting vesicles, in presence of common hermaphroditic duct, in character of vitellaria, as well as relative size and position of testes and ovary. These morphological facts show that the two species are closely related but the differences are too fundamental to permit their inclusion in a single genus.

Alassostoma parvum agrees with A. magnum in general morphological features, presence of oral evaginations, lack of

preoral sphincter, type of lymph and excretory systems, in character of genital systems and presence of hermaphroditic duct, also in relative position of testes and ovary. A. parvum therefore agrees with and differs from S. scleroporum and S. spinulosum in the same manner as A. magnum. That the two forms described are not different developmental stages of the same species is shown by the great difference in the size of the worms and relative differences in size of suckers and genital organs. One of the specimens of A. magnum 10 mm long is not sexually mature while in the sectioned specimen of A. parvum which is less than 3 mm long, spermatozoa were present in the testis and vas deferens. Further, ova were present in the oviduct, and the ootype and anterior part of the uterus were filled with spermatozoa. Eggs were present in only two of the seven specimens of A. magnum and the absence of eggs in the three specimens of A. parvum does not signify that this is a young stage of A. magnum. In view of the agreement of the two American species and the disagreement in many fundamental features from the species described by Looss, a new genus is proposed to contain the present species. A. magnum is large and has small suckers, A. parvum is small and has relatively large suckers and this feature suggested the name Alassostoma.

The genus Alassostoma has the type of lymph and excretory systems present in the genus Schizamphistoma and designated by Looss as characters of the subfamily to which that genus belongs. With the discovery of a second genus, so similar to Schizamphistoma that the two must be included in the same subfamily, the formal erection of the new subfamily is proposed.

Schizamphistoma Looss is designated as type and the name of the new subfamily becomes Schizamphistominae. The subfamily contains the genera Schizamphistoma, the genus to which the species S. spinulosum will probable be removed, and the genus Alassostoma. The characters of the subfamily have been stated by Looss (1912).

The only known form with which the paramphistome from the duck can be compared is Amphistoma lunatum Dies. and it is at once apparent that these two species are very similar. Both are parasites of American ducks , and are the only amphistomes at present known from avian hosts. They are nearly equal in size, are similar in shape, have a sub-terminal oral sucker, the reproductive systems compare very closely, the digestive tracts are similar in character and the acetabula of both are of the same form, consisting of an anterior section and a posterior overhanging lip which terminates on either side in a small cone like projection. A. lunatum has been placed as an anhang to every classification of the amphistomes that has ever been attempted. With the discovery of a form so similar that the two must belong to the same genus, a new genus is proposed to contain the two species. The peculiar divided condition of the acetabulum suggested the name Zygocotyle as appropriate for the genus. A comparison of the two species and a discussion of the genus follows the descriptive section.

Zygocotyle ceratosa n. sp.

The material of this species consists of eight worms from the intestine of Anas platyrhynchos from Rock Co., Nebraska, and is from the collection of Professor H. B. Ward. From the data in the bottle, the contents was the intestine of a duck which had been cut open in places and preserved in formalin. The fixation of the parasites is so poor that the excretory and lymph systems can not be traced, altho remnants of both appear in sections.

Size and Shape. These worms (Fig. 74) vary in length from 3 to 6 mm. and in width from 1.45 to 2.14 mm. In dorsal or ventral aspect they are elongate oval in shape with the acetabulum forming a small terminal projection. In cross section the outline is a flattened oval, which towards the ends of the body becomes more circular. The acetabulum is subterminal, and consists of two parts (Fig. 78), an anterior part extending dorsally and anteriorly into the body, and a posterior overhanging lip which terminates on either side in a little horn or cone like projections 0.12 to 0.2 mm. in length. In the specimen shown in Fig. 74 the opening of the acetabulum is circular, 0.74 mm. in diameter. The cephalic part extends anteriorly 0.46 mm. from the anterior margin of the opening and including the posterior overhanging portion, the opening of the sucker is 1.1 mm. in length.

Body Wall. The cuticula is unarmed, slightly thicker on the dorsal surface. On the ventral surface it is about twelve micra in thickness and on the dorsal surface it is thirty micra. It is not homogeneous, but is traversed by fine crinkled lines extending from internal to external surfaces, and giving it a reticulated appearance. The entire dorsal surface of the body is underlaid with large gland cells, filled with a substance staining deeply with haematoxylin, and whose ducts lead to the dorsal surface. The contents of the gland cells and their ducts have the same appearance and staining reaction as the cuticula of the external surface. The dermo-muscular sac consists of the usual circular, longitudinal and oblique layers, the circular layer is next to the cuticula. From the body wall there are

many large dorso-ventral muscle strands extending thru the body.

Alimentary Tract. The oral sucker is sub-terminal, circular or slightly oval in shape, 0.37 to 0.53 mm. in diameter. The oral evaginations are 0.15 to 0.22 mm. in length and 0.07 to 0.1 mm. broad; they open one on either side from a common sinus (Fig. 76) which opens into the dorsal side of the posterior part of the oral sucker. The esophagus leads from the oral sucker to the intestine: it is 0.05 to 0.37 mm in length and is surrounded by a layer of deeply staining cells. Its caudal portion is surrounded by an esophageal bulb. This structure is oval, 0.2 to 0.45 mm. in length and 0.18 to 0.23 mm. in width, and 0.35 mm. in thickness in the specimen cut in cross sections. It is situated obliquely in the body, the anterior end is ventral and the posterior end more dorsal in position. The muscles are not arranged in concentric lamellae as in the previously described paramphistomes; there is a capsule of external longitudinal fibers and the body of the organ is composed of fibers extending on the sides from the central canal to the external capsule, and above and below the canal the fibers extend across from the lateral walls of the bulb (Fig. 75). The alimentary tract is lined with cuticula to the bifurcation. The ceca are flattened laterally and have lateral lobes which give them a very irregular appearance. They have a muscular wall composed of circular and inner longitudinal fibers; and extend posteriad almost to the opening of the acetabulum, terminating just caudad of the excretory pore.

<u>Male Reproductive Organs</u>. The testes lie one behind

one another in the median line, the caudal testis is almost in the center of the body, and the cephalic testis is about 0.[illegible] mm. in front of it. They are about the same size, lobulated, oval, crosswise of the body, almost touching the ceca of either side. They are ventral in position, almost touching the ventral body wall and not extending far into the dorsal half of the worm. They vary in size from 0.2 mm by 0.3mm. in the smallest to 0.55 by 0.78 mm. in the largest specimen. The vasa efferentia arise from the anterior dorsal margins, the right tube from the anterior and the left tube from the posterior testis. Near the genital pore they unite and form a much coiled seminal vesicle which has a thickened muscular wall. The terminal part that leads ventrad to the genital pore is expanded and the walls are thinner, and this part is surrounded by the cells of the prostate gland. A cirrus sac and cirrus are absent, the male and female tubes open to the exterior separately at the apex of a slight ventral prominence. The opening of the male duct is immediately anterior to that of the female (Fig. 80). The seminal vesicle extends thru twenty five ten micra sections.

<u>Female</u> <u>Reproductive</u> <u>Organs</u>. The ovary is oval, lobulated, crosswise of the body, about the shorter diameter of the caudal testis behind it. In the smallest specimen it is 0.[illegible] by 0.28 mm. and in the largest it is 0.[illegible] by 0.52 mm. The oviduct arises at the dorsal margin as a very small tube and passes dorsad where Laurer's canal is given off. This canal passes in short curves to the dorsal surface, opening anterior to the excretory pore. After giving off Laurer's canal the oviduct passes posteriad and ventrad into the Mehlis' gland where a short common

vitelline duct is received. The uterus coils irregularly in close folds from the Mehlis' gland to the genital pore. The uterine coils are largely in the dorsal part of the worm, altho they may pass into the ventral portion and coil around the testes. Laterally the coils of the uterus are limited by the ceca. The terminal part has a slight thickening of the wall but not a distinctly delimited metraterm. The vitellaria are well developed, large follicles extending in the extracecal areas from the level of the posterior edge of the oral sucker to the anterior edge of the opening of the acetabulum. They are limited medially by the ceca and laterally they extend almost to the body wall. They are more ventral than dorsal in position. Eggs are present in large numbers. In size they average 0.14 by 0.083 mm.

Tabulated comparison of the species Z. lunata and Z. ceratosa.

Length.

Z. lunata, 3 to 9 mm.

Z. ceratosa, 3 to 6 mm.

Width.

Z. lunata, 1 to 3 mm.

Z. ceratosa, 1.45 to 2.14 mm.

Oral sucker.

Z. lunata, 0.4 to 0.5 mm.

Z. ceratosa, 0.37 to 0.53 mm.

Oral evagiantions.

Z. lunata, 0.3- 0.35 mm. long; 0.1- 0.12 mm. wide.

Z. ceratosa, 0. 15 -0.22 mm. long; 0.07 -0.1 mm. wide.

Esophagus.

Z. lunata, 1 to 1.3 mm, long.

Z. ceratosa, 0.05 to 0.37 mm. long.

Esophageal bulb.

Z. lunata, 0.2 mm. in diameter.

Z. ceratosa, 0.2 -0.45 mm. long; 0.18 -0.23 mm. broad.

Ceca.

Z. lunata, extend to anterior wall of acetabulum or 1 mm. anterior to it.
Z. ceratosa, 0.1 to 0.15 mm between ends of ceca and anterior wall of acetabulum.

Testes.

Z. lunata, circular, lobed, 0.5 mm. in diameter.

Z. ceratosa, oval, lobed, 0.2 by 0.3 to 0.55 by 0.78 mm.

Ovary.

Z. lunata, circular, 0.3 mm in diameter.

Z. ceratosa, oval, lobed, 0.2 by 0.33 to 0.33 by 0.52 mm.

Vitellaria.

Z. lunata, from oral to ventral suckers, both extra and intra-cecal.
Z. ceratosa, from oral sucker to acetabulum, extracecal.

Eggs.

Z. lunata, 0.145 -0.15 by 0.072 -0.075 mm.

Z. ceratosa, 0.14 by 0.083 mm.

Host.

Z. lunata, three species of the genus Anas, Himantopus wilsonii, South America
Z. ceratosa, Anas platyrhynchos, North America.

Z. ceratosa is thicker, the acetabulum is much nearer the ovary, the oral evaginations are smaller, the esophagus is shorter, the testes and ovary are oval and larger, and the vitellaria are entirely extracecal while in Z. lunata they extend between the ceca.

The species Z. lunata was described by Diesing (1836); the material was collected by Natterer in Brazil during a South American expedition from the cecum of Anas melanotus, A. ipecutiri, A. moschata fer., Himantopus wilsonii, and from the cecum of Cervus dichotomus. Fischoeder secured the original specimens from the Vienna museum and (1903) gave a more extended description of the form, altho his study was restricted to the examination of toto preparations. Fischoeder states that the citation of Cervus dichotomous as a host of this form is probably an error, and the same suspicion was mentioned by Diesing (1850).

As diagnostic characters of the genus Zygocotyle may be mentioned the sub-terminal oral sucker, posterior sucker divided or provided with a caudal overhanging lip, the absence of cirrus sac and cirrus, and the separate openings of the male and female ducts. Others will undoubtedly appear when the character of the excretory and lymph systems are known. The genus Zygocotyle differs from all other known genera of the Paramphistomidae in the ventral position of the oral sucker and the peculiar character of the acetabulum. It differs from the Gastrodiscinae in the shape of body and absence of ventral papillae, and from the Gastrothulacinae in the absence of the ventral pouch. In the lobed testis and absence of cirrus sac it agrees with the Paramphistominae, but the oral evaginations exclude it from this group. The absence of cirrus sac and lobed form of the testes will not permit its inclusion with the Cladorchinae. The characters of the Diplodiscinae are so poorly defined that a comparison is unsatisfactory; in this group however, a cirrus sac is present and both suckers are terminal. None of the existing sub-families

this group is necessary to establish its validity and determine its diagnostic features. Stiles and Goldberger (1910) proposed a new classification of the group, but as has already been pointed out, the arrangement is based on superficial and minor characters. The subfamily Gastrothylacinae created by these authors appears to be clearly distinguished by the presence of the large ventral pouch and should be retained. Looss (1902) described the lymph system of A. spinulosum and (1912) considers the lymph and excretory systems of major importance in classification. As characters of the new family Schizamphistominae he mentioned the type of lymph and excretory systems. Since the lymph system is not described in other subfamilies, the former diagnoses based on body form, types of digestive and reproductive systems, presence of ventral pouch, etc., must for the present be retained. Since so many of the forms are incompletely described, and considerable difference of opinion has existed in regard to the taxonomic value of the different features, the classification of the entire group is uncertain. Looss (1912) says, " Jeder Klassifikationsversuch, der den Bau der Excretions- und Lymphgefässsystem ausser acht lässt, mag sich wohl einen Klassifikationsversuch nennen, kann aber niemals Anspruch darauf erheben, als natürlicher oder (was dasselbe ist) wissenschaftlicher Klassifikationsversuch angesehen zu werden." In the same article he states, " Ich deutete schon weiter oben an, dass ich vor mehreren Jahren eine Revision des mir verfügbaren Amphistomenmaterials begonnen, aber bis jetzt nicht zu Ende gebracht habe. Meine Aufmerksamkeit richtete sich selbstverständlich zuerst auf diejenigen Organe, die ich in systematischer

will include the genus, and it is probable that it is a member of an as yet unknown sub-family. Since the present classification of the Paramphistomidae is somewhat uncertain, and the structure of the excretory and lymph systems of this genus is unknown, no further attempt at classification is made at this time.

Our present knowledge of the Paramphistomidae is largely the result of the work of Monticelli, Otto, Fischoeder, Cohn, Daday, Stiles and Goldberger, Looss and Odhner.

The first division of the group was made by Monticelli (1892) when he separated Gastrodiscus from the rest and created the subfamily Gastrodiscinae. Fischoeder in a series of papers described several species from mammals, and (1903) formulated the second scheme of classification. He created two subfamilies; Paramphistominae, in which the testes are lobed, and paired oral evaginations and cirrus sac are absent; and Cladorchinae, characterized by the branched testes, and the presence of paired oral evaginations and cirrus sac. Recent additions to our knowledge of the family have rendered it difficult to use these distinctions. Cohn (1904) created the family Diplodiscinae to contain the species Diplodiscus, Opisthodiscus and Catadiscus. As diagnostic characters he states," Amphistomiden von gedrungener, konischer Form und rundem Querschnitt. Mundsaugnapf gut ausgebildet, mit zwei retrodorsal Taschen. Ein grosser Endsaugnapf, über welchem dorsal der Excretionsporus liegt. Mundöffnung terminal, Darmschenkel bis zu Endsaugnapf reichend, relativ sehr breit. Leben im Enddarm von Amphibien und Reptilien." This characterization is inadequate, since the anatomical features are shared by almost half the members of the family, and obviously further study of

Hinsicht für bedeutungsvoll hielt, d.i. den allgemein Bau des Lymph- und Exkretionsapparates und den feineren Bau der Genitalend-organe, auf dieselben Organe also, die von den früheren Autoren (bis dahin kam nur Fischoeder in Frage) ausser acht gelassen worden waren. Es stellte sich bald heraus, dass der feinere Bau der Genitalendteile ein gutes, je fast das einzige, sichere Unterscheidungsmerkmal ähnlicher Arten ist, während Exkretions- und Lymphapparat durch alle untersuchten Formen hindurch im Prinzip übereinstimmende Verhältnisse zeigten."

The only arrangements of the genera of the family are those of Fischoeder and Stiles and Goldberger. The classification of Fischoeder is almost entirely outgrown and that of Stiles and Goldberger was never accepted, but for sake of completeness both are included.

Classification of Fischoeder 1903.

Paramphistomidae

Paramphistominae
- Gastrothylax
- Paramphistomum
- Stephanopharynx
  - Species inquirende, A. gigantocotyle
  - A. explanatum

Cladorchinae
- Gastrodiscus
- Homalogaster
- Diplodiscus
- Cladorchis
- Chiorchis
  - Species inquirende, A. hawkesi, A. collinsi, A. ornatum, A. papillatum, A. tuberculatum, A. emarginatum, and A. lunatum.

Balanorchis

Classification of Stiles and Goldberger 1910.

Paramphistomoidea

Gastrodiscidae
Gastrodiscus
Homalogaster

Gastrothylacidae
Gastrothylax
Wellmanius
Carmyerius
Fischoederius

Paramphistomidae

Paramphistominae
Paramphistomum
Cotylophoron

Cladorchinae
Cladorchis
Taxorchis
Pseudodiscus
Watsonius
Pseudocladorchis
Microrchis
Chiorchis
Balanorchis
Pfenderius

Diplodiscinae
Diplodiscus
Catadiscus
Opisthodiscus

Stephanopharynginae
Stephanopharynx

In lieu of further researches , the present status of the group and its subdivisions is complied from the literature and given as a tentative arrangement.

Paramphistomidae Fischdr. 1901

Gastrodiscinae Montic. 1892
- Gastrodiscus
- Homalogaster

Paramphistominae Fischdr. 1901
- Paramphistomum
- Stephanopharynx
- Cotylophoron

Cladorchinae Fischdr. 1901
- Cladorchis
- Taxorchis
- Chiorchis
- Pseudodiscus
- Microrchis
- Pseudocladorchis
- Watsonius
- Pfenderius

Diplodiscinae Cohn 1904
- Diplodiscus
- Opisthodiscus
- Catadiscus

Gastrothylacinae Stiles and Goldberger 1910
- Gastrothylax
- Wellmanius
- Carmyerius
- Fischoederius

Schizamphistominae n. subfam.
- Schizamphistomum
- Alassostoma

Genera of uncertain position
- Balanorchis
- Zygocotyle

# VI. Phylogenetic Considerations.

The study of the Polystomidae shows unusual morphological variation in that group. This might be explained by the theory of convergence so well stated by Richard Hertwig in his Manual of Zoology, (Kingsley) p. 157; here he says, " In case of entoparasites the transforming influence of parasitism is so considerable that representatives of the most diverse groups take on a remarkable similarity of appearance and structure.... Entoparasitism is therefore one of the best examples for illustrating convergent development, i.e. animals of different systematic position acquiring, under similar conditions of life, a great similarity of structure and appearance." Pratt (1908) reviews the literature and arguments for this theory which are based on trematode morphology. S. J. Johnston (1914) argues for divergence as the true explanation of the variation of the species of Pneumonoeces, Gorgoderinae, Brachycoeliinae, etc, and believes that the solution of the problem may be sought in the study of the relationships of the distribution of trematode parasites and the distribution of their hosts.

Whether the likenesses and differences in the structure of present species are the result of convergence or divergence, it seems that the distributional factor emphasized by Johnston is not of major importance. Parasitic distribution could precede the distribution of the primary and secondary hosts only in case the parasites changed to new primary or secondary hosts. But today more than one species may serve as primary or secondary host; the parasite is probably in a restricted degree able to adapt its physiological life history so other species may serve as hosts, and primitively this adaptability may have been greater than now.

The parasitic distribution certainly varies to a large extent with the distribution of the primary host, and to a less extent with the distribution of the secondary host, but the presence of two similar forms in the same region does not prove whether their hosts had primitively the same or different parasites. The question of whether the peculiar life history of the parasite would favor or restrict migration is not of importance in this connexion for the same factors would probably influence to the same effect, either the same diverging or two converging species. The life history of the trematodes is so imperfectly known that at present no fianl decision can be formed on this basis.

Considerable light is thrown on this subject by the recent studies of Odhner on a natural system of the digenetic trematodes. He strongly advocates that the monostomes are a group which lack close relationships and have no familial entity, but consist of forms derived from various distome groups which have converged in the direction of a single oral sucker. Pointing out close and fundamental agreement he argues that the monostome family Angiodictyidae is really a subfamily of the Amphistomidae. He shows essential morphological agreement between Dist. quadrangulum Daday and the fish amphistomes. His examination of the original of Aspidocotyle confirmed the statement of Braun (1893) that this form belongs to the amphistomes, altho its relation to the other members of the group is uncertain. Further he states that the cercaria of Gasterostoma in the structure of the oral sucker and the presence and relations of the oral evaginations shows that this form doubtless belongs to the Amphistomidae. His derivation of the Gasterostoma from

amphistome like forms of frogs is plausibly explained since the frogs serve as food for the hosts of the gasterostomes. The structural comparisons of Odhner appear to show very clearly that convergence and divergence have both had great influence in the phylogeny of certain trematode families, e. g. convergence toward a single oral sucker and divergence from the amphistome stem.

The present wide variation in the structure of the members of the genus Polystoma can not be adequately explained thru differences in distribution, age of parasite, host or location in the host. In the genus so far as is known, the long uterus containing many eggs is confined to species infesting the urinary bladder of amphibian hosts of the old world, however, in other characters e. g. the shape of the caudal disc and the absence of great hooks, these amphibian forms of the Eastern hemisphere disagree with each other and agree with forms parasitic in the urinary bladder and oral cavity of North American turtles. These turtle parasites have a very similar structure, whether parasitic in the urinary bladder or pharyngeal cavity. Furthermore if the observations of Zeller are correct, and individuals of P. integerrimum becoming mature in the gills of frog larvae lack external vaginae, and have a spherical testis and and a single egg in the uterus, we are entirely at a loss to explain the variation existing in the genus.

In the Aspidogastridae, the young individuals have an oral sucker, a small posterior acetabulum without dividing ridges, and very closely resemble young distomes. The mode of infection is almost entirely unknown, and this offers a promising field for investigation. The discovery of the sexual form of

Stichocotyle by Odhner (1898) establishes the fact that at least one species of the Aspidogastridae has an intermediate host. Nickerson (1902) observes," owing to the well known tendency of fresh water conditions to obliterate larval life, it may well be that Aspidogaster has secondarily lost a more or less complicated series of changes, which have been retained by its relatives inhabiting salt water,". The presence within the family of both monogenetic and metastatic development, together with other characters common to both Heterocotylea and Malacocotylea designate it as an intermediate group. The morphological structure is similar to that of the Malacocotylea while the development is similar to that of the Heterocotylea. Whether or not the Aspidogastridae are primitive or secondarily degenerate forms is as yet undecided. The simple and archaic character of the intestine, the eye spots, the direct development and the ectoparasitic habit as it occurs in the family, and the parasitic infection of molluscs by adult forms strongly suggests a very primitive and ancient group. It is probable that complete evidence concerning the structure and life history of this family would go a long way toward solving the problem of whether the invertebrate or the vertebrate is the original host and the attendant problem of the origin of double hosts.

The trematodes are generally regarded as descended from a turbellarian like ancestor which possessed a posterior sucker. With the assumption of the parasitic habit adaptations began in various directions. The difference in type of adhesive apparatus may in a general way be explained thru differences in habit. The oral sucker has developed thru continued adhesion by the

anterior end, both in attachment for locomotion and in securing food. In Gasterostoma the mouth is on the ventral surface and an anterior adhesive sucker is developed, altho this is probably a secondary feature. In response to the constant necessity for strong adhesion, the ectoparasites have developed accessory posterior organs of attachment, while in most of the entoparasitic forms the acetabulum has migrated anteriad or disappeared entirely. The ectoparasitic forms retained many of their former characters, while added protection and food supply, afforded those specializing toward entoparasitic existence, provided for perpetuation and distribution of the species in the excessive development of the reproductive apparatus. In the Heterocotylea the posterior sucker has been replaced by a disc which bears suckers and hooks, in the Aspidocotylea the acetabulum has specialized into a multiloculate adhesive organ, in the distomes it has migrated anteriad, and in the monostomes disappeared entirely. In the young of many of these forms there is a single posterior sucker which fact adds weight to the theory that present groups are descended from a primitive form with a simple posterior sucker.

The Paramphistomidae appear to be a primitive family of the distomes that have retained the primitive caudal sucker, altho certain species show specializations of the organ. The work of Odhner shows that the gasterostomes, Aspidocotyle, and certain monostomes are branches from the amphistome stem. The divided condition of the body in Gastrodiscus recalls the similar condition in the Aspidogastridae, and suggests a possible relationship between these families. At the present time our knowledge of the Paramphistomidae and its relationships is in an uncertain condition, and further work on this family is

necessary before any comprehensive attempt at classification can be made.

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## EXPLANATION OF PLATES.

All figures except those of reconstructions were drawn with the aid of the camera lucida.

Abbreviations used.

| | | | |
|---|---|---|---|
| a | acetabulum | mo | marginal organ |
| as | anterior sucker | mt | metraterm |
| cm | circular muscles | nc | nerve commissure |
| cs | cirrus sac | o | ovary |
| e | esophagus | oc | eye |
| eb | esophageal bulb | od | oviduct |
| eg | egg | oe | oral evagination |
| et | excretory duct | om | oblique muscles |
| ex | excretory pore | oo | ootype |
| g | genital pore | ood | ooduct |
| gc | genito-intestinal canal | os | oral sucker |
| gn | ganglion cell | p | prostate gland |
| h | small hooklets | ph | pharynx |
| hd | hermaphroditic duct | sp | septum |
| i | intestine | t | testis |
| l | Laurer's canal | ut | uterus |
| lm | longitudinal muscles | v | vitellaria |
| ls | lymph sinus | vd | vas deferens |
| lt | limiting membrane | vg | vagina |
| m | mouth | vl | vitelline duct |
| mg | Mehlis' gland | vv | vitello-vaginal canal |
| md | median dorsal lymph canal | | |
| mv | median ventral lymph canal | | |

PLATE I

Fig. 1. Polystoma orbiculare, extended, ventral view; x35.

Fig. 2. P. orbiculare, frontal section thru anterior sucker,pharynx and anterior part of intestine; x 44.

Fig. 3. P. orbiculare, frontal section thru pharynx; x 140.

Fig. 4. P. orbiculare, sagittal section thru anterior part of alimentary tract; x 90.

Fig. 5. P. orbiculare, frontal section; x 35.

Fig. 6. P. orbiculare, primary ducts of vitellaria; x 135.

Fig. 7. P. orbiculare, frontal section caudal disc; x 73.

Fig. 8. P. orbiculare, sagittal section thru cecum; x 45.

PLATE II

Fig. 9. P. orbiculare, frontal section thru region of the ootype; x 235.

Fig. 10. P. orbiculare, frontal section of ootype, same specimen as Fig. 9; x 235.

Fig. 11. P. orbiculare, reconstruction of male genital apparatus from sagittal sections; x 140.

Fig. 12. P. orbiculare, section thru uterus; x 700.

Fig. 13. P. orbiculare, frontal section thru genital sinus; x 135.

Fig. 14. P. orbiculare, frontal section just dorsad of that shown in Fig. 13; x 135.

Fig. 15. P. orbiculare, hook from genital coronet; x 225.

Fig. 16. P. orbiculare, reconstruction of genital apparatus from frontal sections; x 135.

Fig. 17 P. hassali, reconstruction of genital apparatus from frontal sections; x 135.

PLATE III

Fig. 18. Polystoma opacum, ventral view; x 20.

Fig. 19. P. opacum, frontal section thru mouth funnel and pharynx, showing nerve commissures and vitellaria; x 60.

Fig. 20. P. opacum, frontal section thru brain, showing large ganglion cells.

Fig. 21. P. opacum, hook from genital coronet; x 550.

Fig. 22. P. opacum, reconstruction of genital apparatus from toto and cross sections; x 50.

Fig. 23. P. opacum, cross section thru uterus and cirrus sac; x 60.

Fig. 24. P. opacum, cross section thru testis; x 60.

Fig. 25. P. opacum, cross section thru anterior pair of bothria; x 60.

PLATE IV

Fig. 26. P. megacotyle, ventral view; x 27.

Fig. 27. P. megacotyle, cross section of pharynx; x 85.

Fig. 28. P. megacotyle, cross section thru cirrus sac, showing the insertion of the genital hooks; x 140.

Fig. 29. P. megacotyle, cross section thru ootype; x 70.

Fig. 30. P. megacotyle, cross section thru ovary and uterus; x 85.

Fig. 31. P. megacotyle, cross section thru cirrus sac; x 140.

PLATE V

Fig. 32. P. microcotyle, ventral view; x 27.

Fig. 33. P. hassali, frontal section thru dorsal part of uterus; x 60.

Fig. 34. P. hassali, ventral view, showing posterior connexion of the ceca; x 45.

Fig. 35. P. microcotyle, ventral view of caudal disc, showing arrangement of musculature and hooks; x 48.

Fig. 36. P. hassali, ventral view; x 40.

Fig. 37. P. coronatum Leidy, ventral view; x 27.

PLATE VI

Fig. 38. P. orbiculare, bothrium from caudal disc; x 140.

Fig. 39. P. orbiculare, frontal section thru bothrium; x 140.

Fig. 40. P. orbiculare, optical section thru bothrium, showing cuticular framework; x 140.

Fig. 41. P. opacum, hook from base of sucker; x 165.

Fig. 42. P. opacum, hook from anterior margin of caudal disc; x 165.

Fig. 43. P. microcotyle, hooks from posterior margin of caudal disc; x 165.

Fig. 44. P. opacum, hooks from posterior margin of caudal disc; x 165.

Fig. 45. P. megacotyle, hooks from posterior margin of caudal disc; x 165.

Fig. 46. P. coronatum, hooks from posterior margin of caudal disc; x 165.

PLATE VI

Fig. 47. P. orbiculare, hook from base of sucker; x 155.

Fig. 48. P. orbiculare, frontal section thru bothrium, illustrating method of operation; x 140.

Fig. 49. P. integerrimum, frontal section thru bothrium, showing type of cuticular framework different from that illustrated in the other figures; x 100.

PLATE VII

Fig. 50. Cotylaspis cokeri, extended, dorsal view; x 40.

Fig. 51. C. cokeri, ventral view, showing the position of the marginal organs and the divisions of the adhesive disc; x 40.

Fig. 52. C. cokeri, contracted, dorsal view; x 40.

Fig. 53. C. cokeri, diagrammatic representation of excretory system, from living specimen, dorsal view; x 40.

Fig. 54. C. cokeri, cross section thru ovary; x 85.

Fig. 55. C. cokeri, reconstruction of reproductive organs from frontal sections; x 80.

Fig. 56. C. cokeri, frontal section thru adhesive disc, showing arrangement of musculature; x 95.

PLATE VIII

Fig. 57. Cotylaspis cokeri, sagittal section thru the anterior end, showing musculature, digestive, reproductive and marginal organs; x 200.

Fig. 58. C. cokeri, frontal section thru region of the genital pore; x 180.

Fig. 59. C. cokeri, frontal section thru mouth funnel; x 300.

Fig. 60. C. cokeri, cross section anterior part of pharynx, showing nerve commissures and eye spots; x 160.

PLATE IX

Fig. 61. Alassostoma magnum, ventral view; x 9.

Fig. 62. A. magnum, cross section at level of ovary; x 16.

Fig. 63. A. magnum, cross section thru oral evaginations, x 40.

Fig. 64. A. magnum, section of wall of cecum; x 360.

Fig. 65. A. magnum, reconstruction of female genital apparatus from cross sections; x 40.

Fig. 66. A. magnum, cross section thru genital pore; x 37.

Fig. 67. A. magnum, cross section thru the oral sucker; x 35.

## PLATE X

Fig. 68. Alassostoma parvum, ventral view; x 27.

Fig. 69. A. parvum, cross section thru genital pore; x 30.

Fig. 70. A. parvum, cross section esophageal bulb; x 70.

Fig. 71. A. parvum, cross section thru seminal vesicle; x 70.

Fig. 72. A. parvum, cross section posterior to ovary, showing excretory ducts; x 70.

Fig. 73. A. parvum, cross section thru acetabulum; x 70.

## PLATE XI

Fig. 74. Zygocotyle ceratosa, ventral view; x 11.

Fig. 75. Z. ceratosa, cross section esophageal bulb; x 45.

Fig. 76. Z. ceratosa, cross section thru origin of oral evaginations; x 45.

Fig. 77. Z. ceratosa, sagittal section thru anterior part of body; x 27.

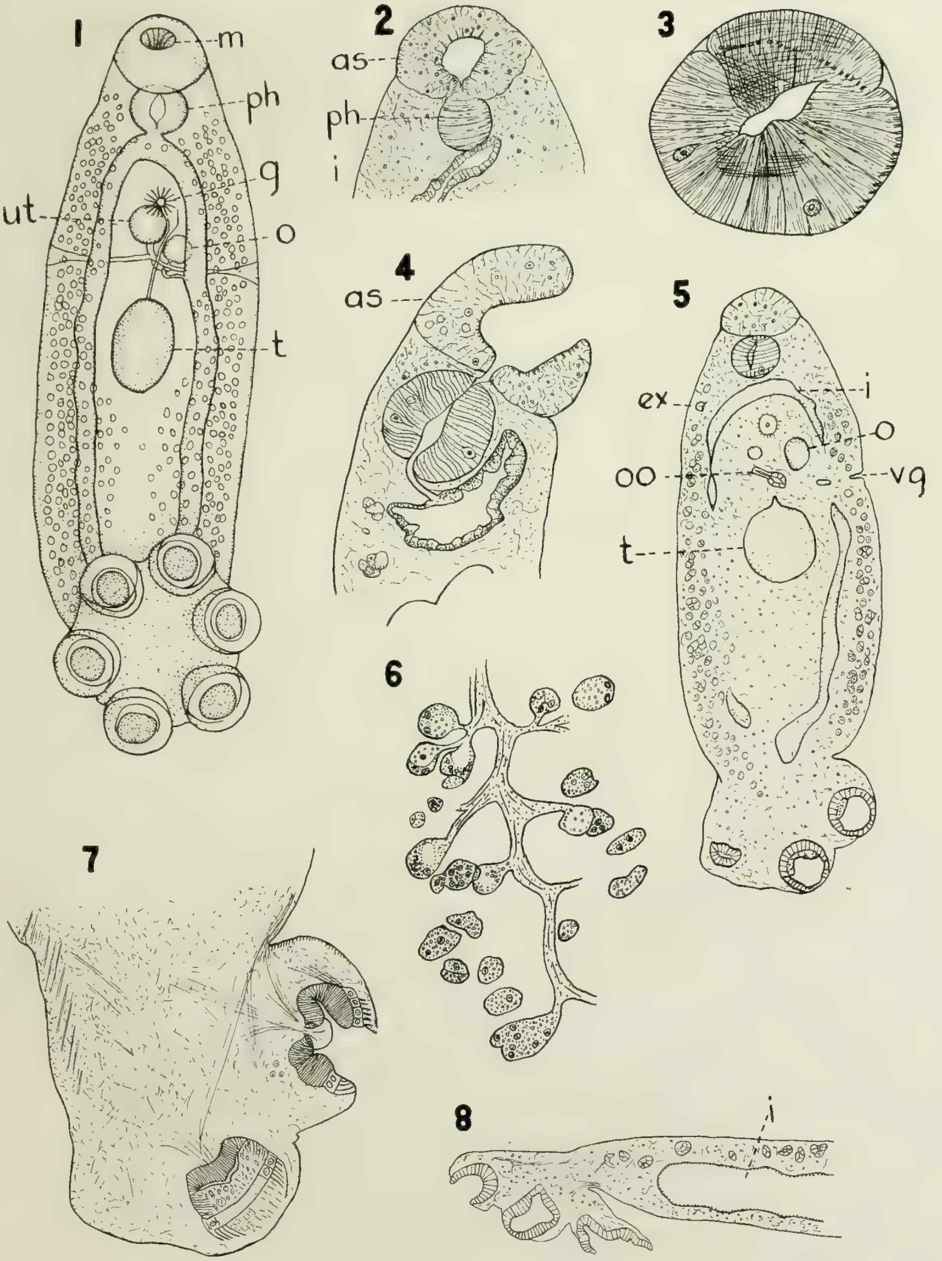
Fig. 78. Z. ceratosa, sagittal section thru the posterior part of body; x 27.

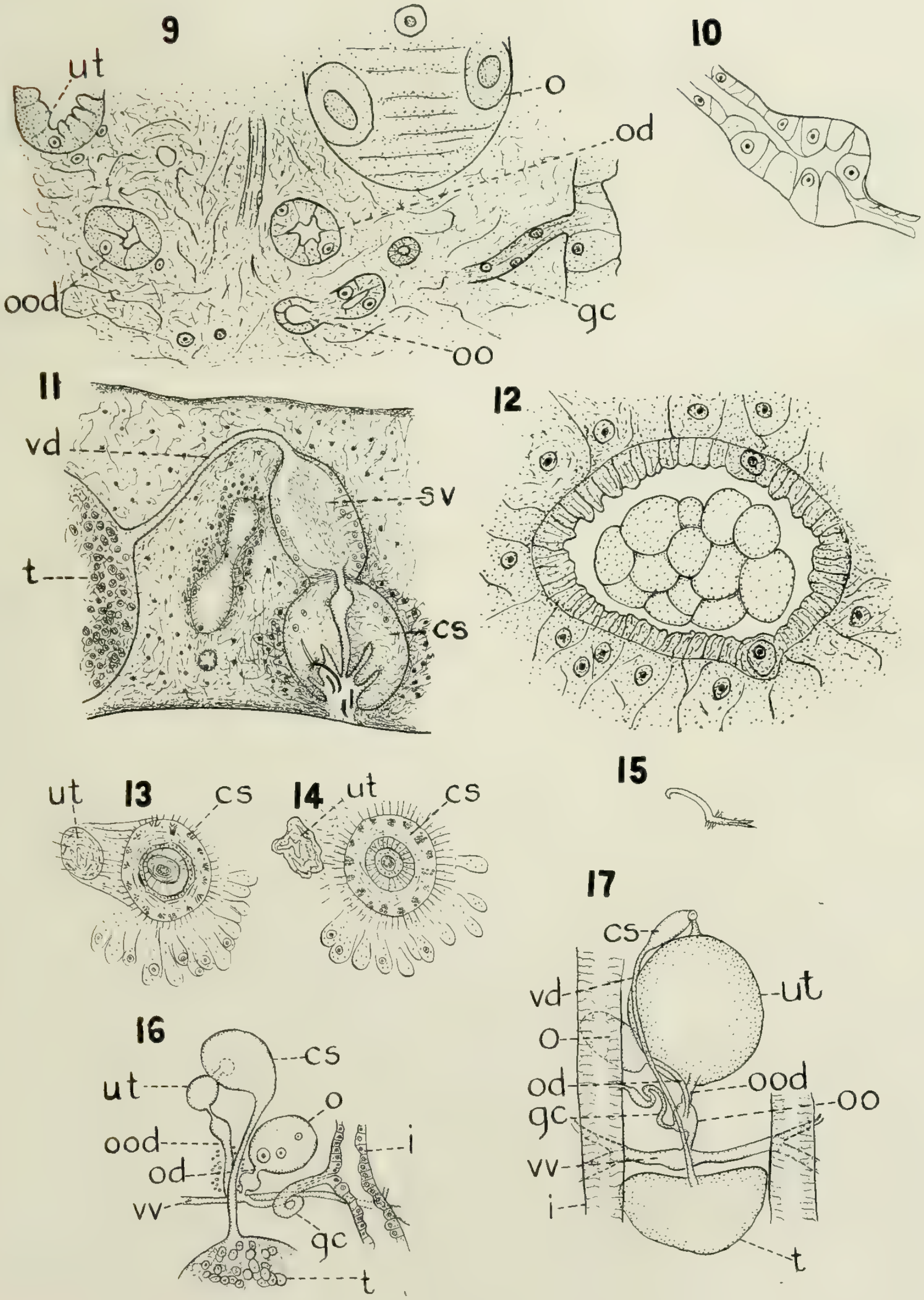
Fig. 79. Z. ceratosa, sagittal section thru lateral part of acetabulum.

Fig. 80. Z. ceratosa, sagittal section thru genital pore; x 100.

Fig. 81. Z. ceratosa, sagittal section thru openings of Laurer's canal and the excretory vesicle; x 90.

PLATE I

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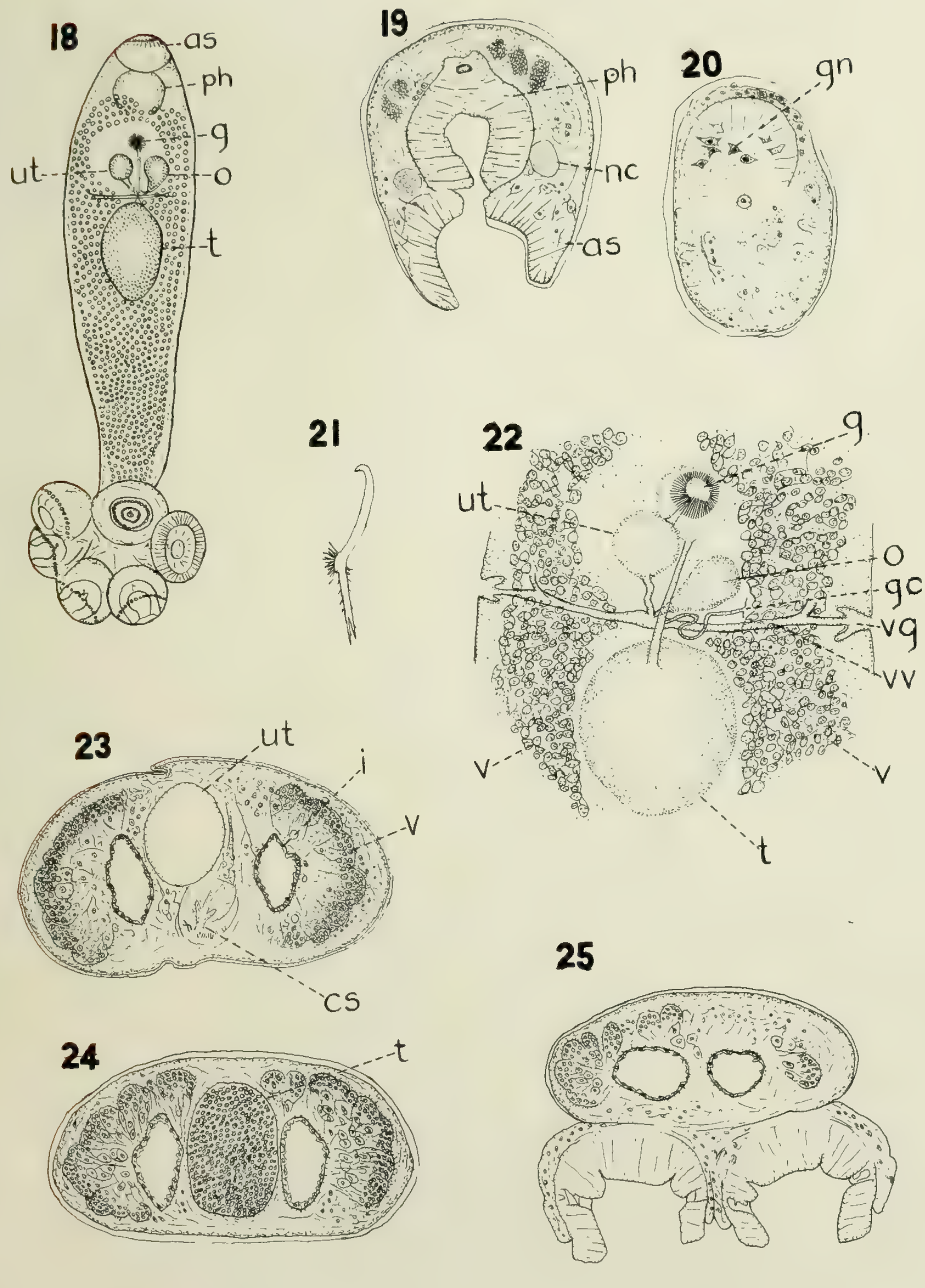
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PLATE IV

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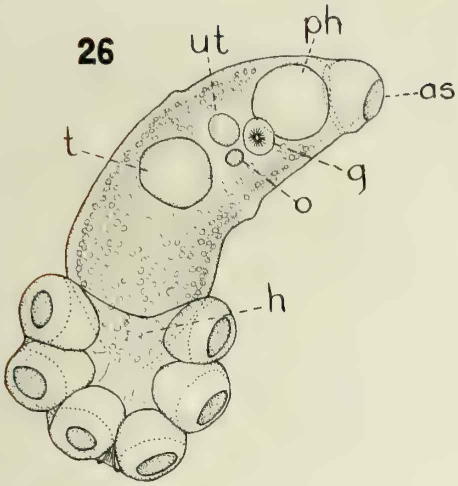


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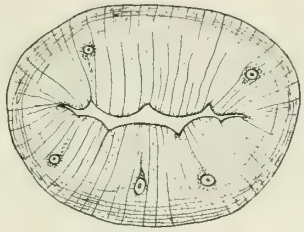

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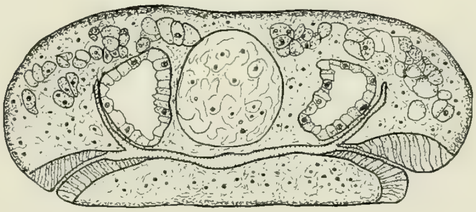

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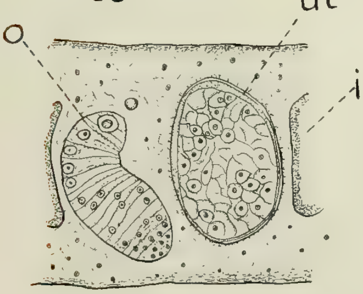


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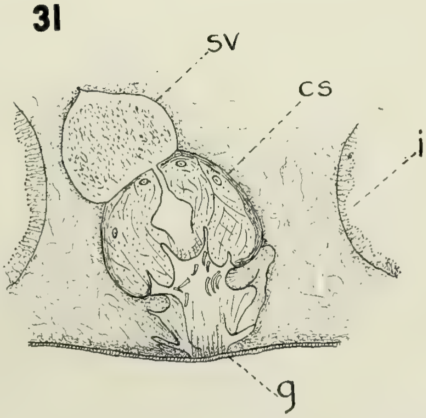

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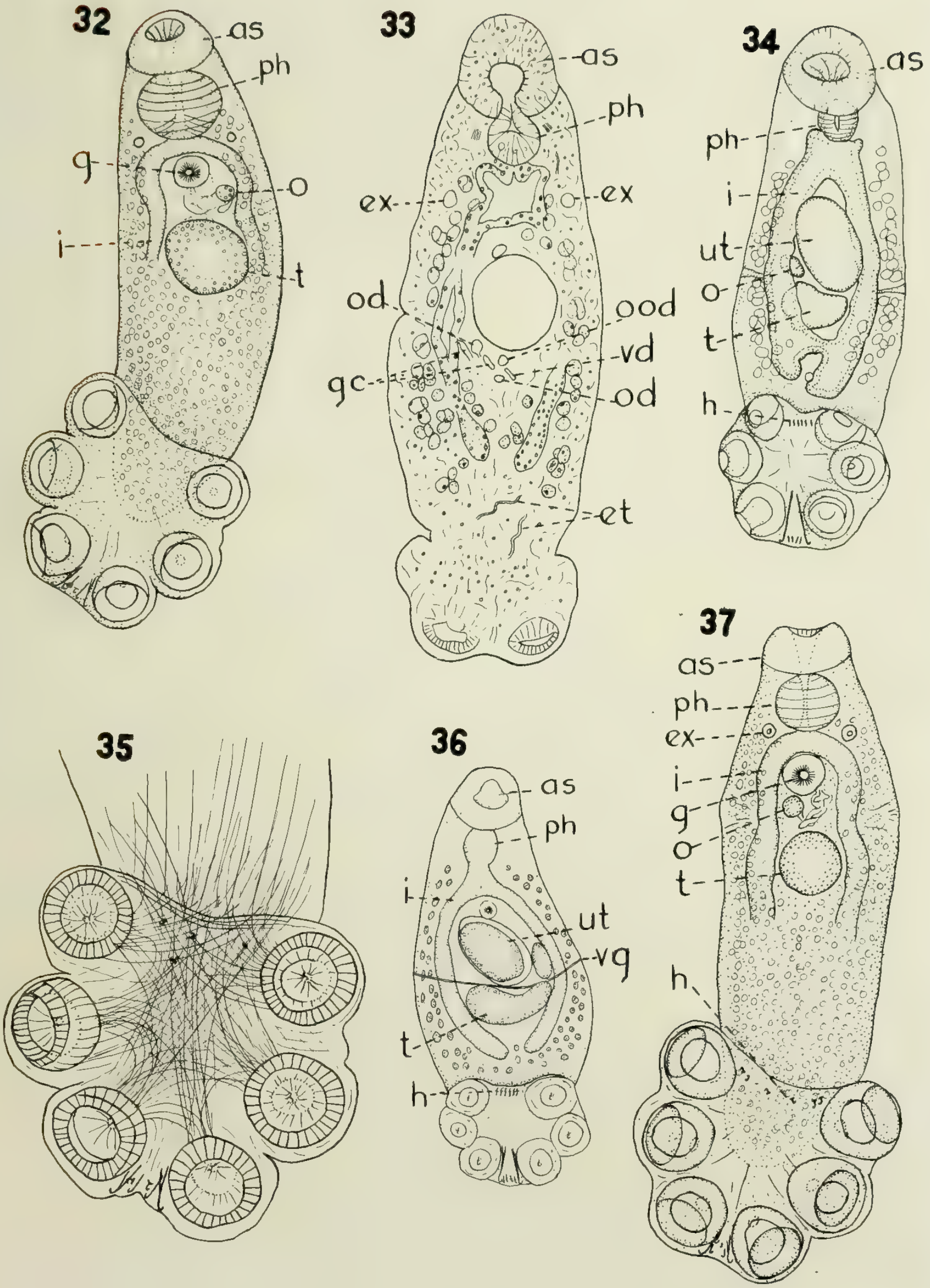
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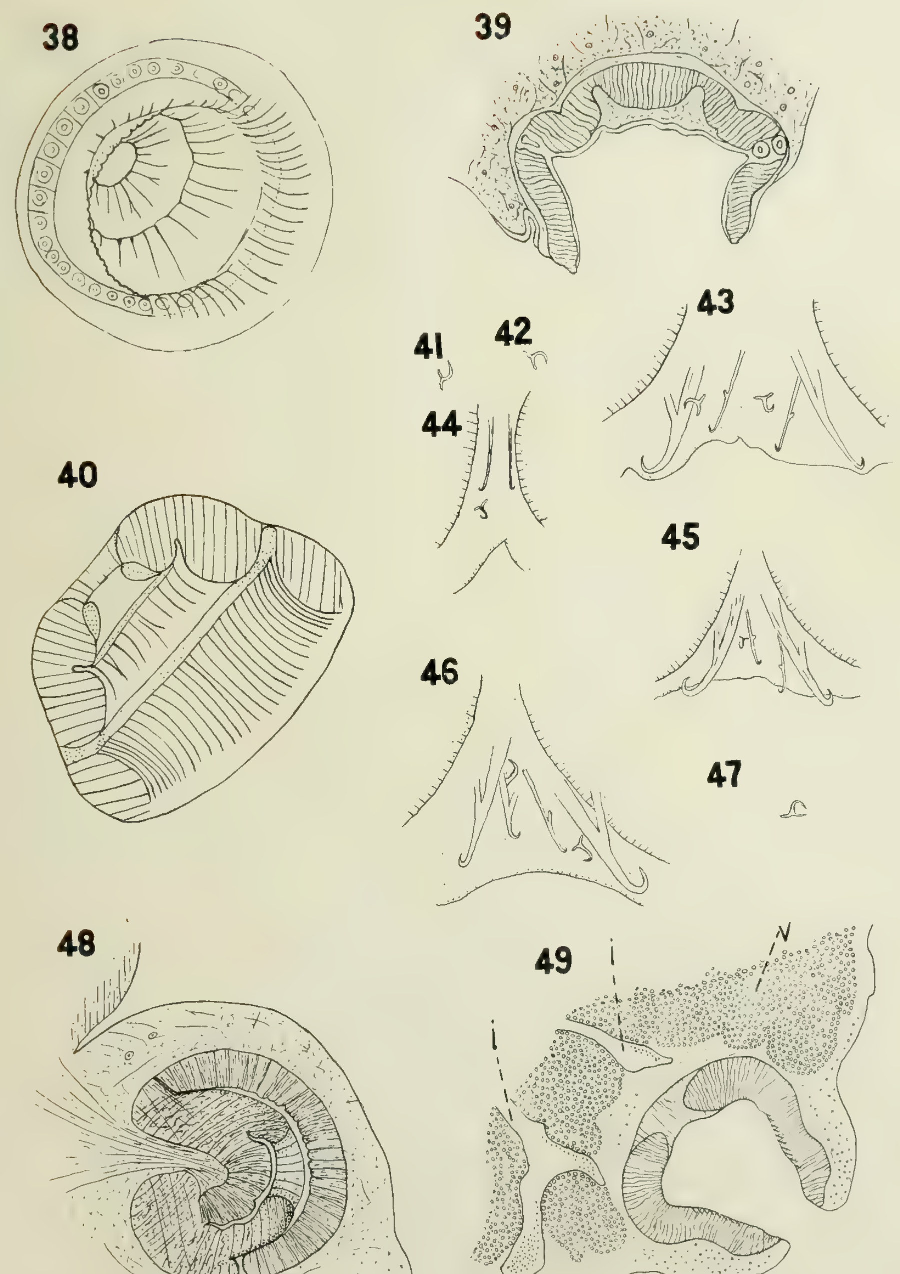

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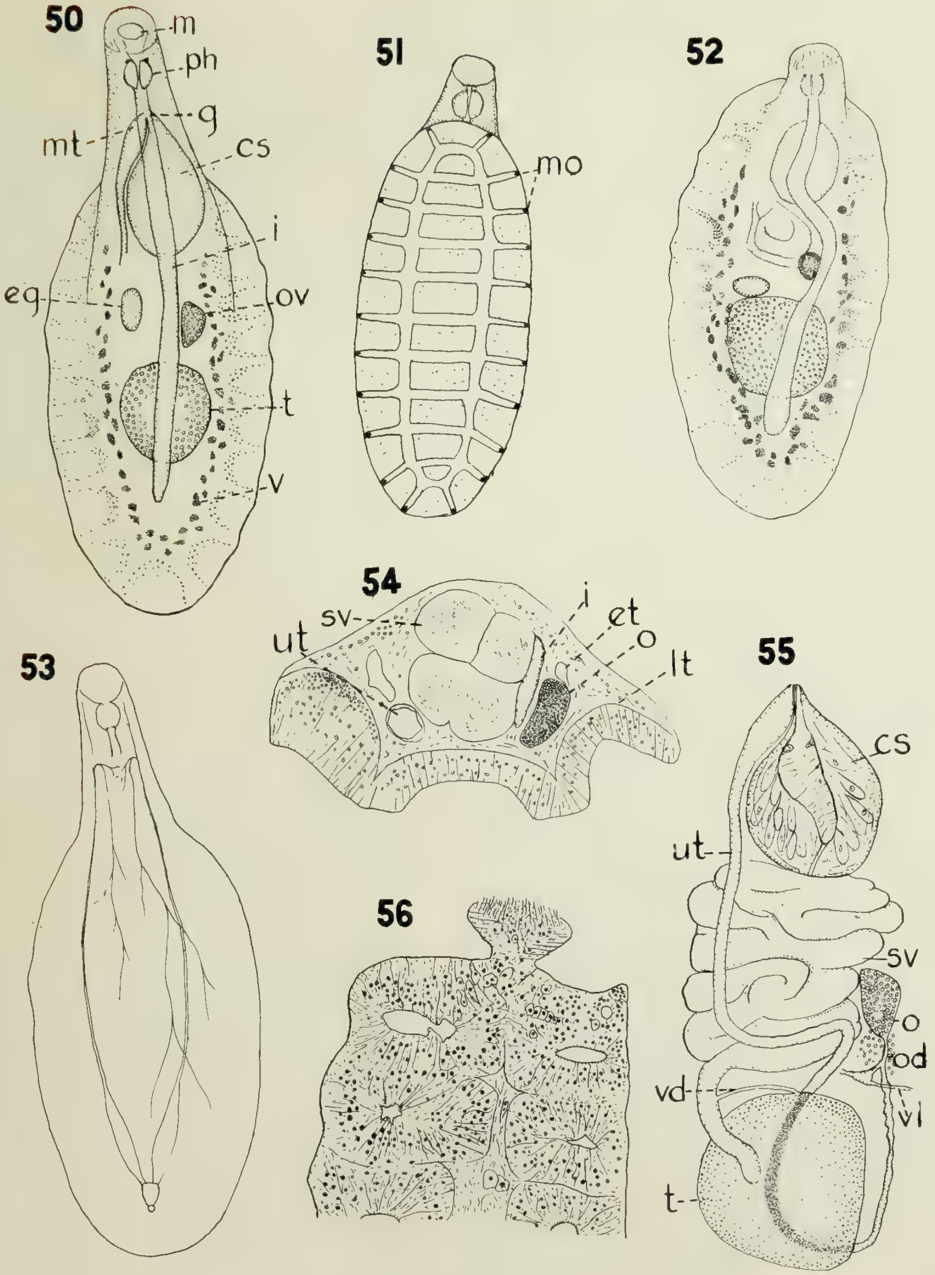
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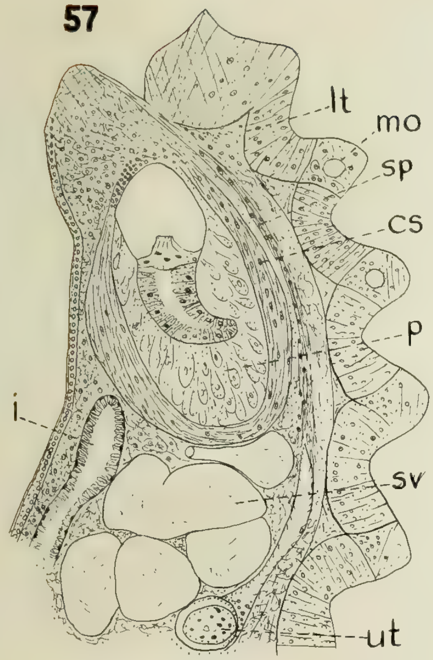


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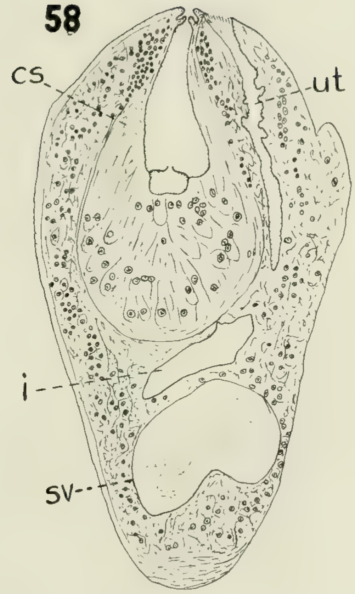


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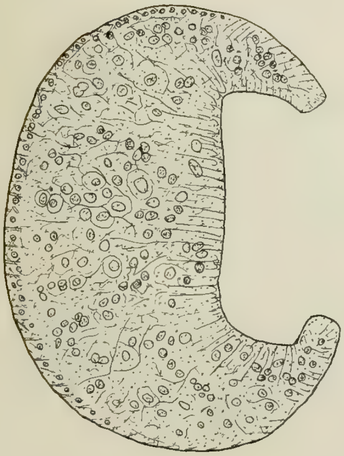

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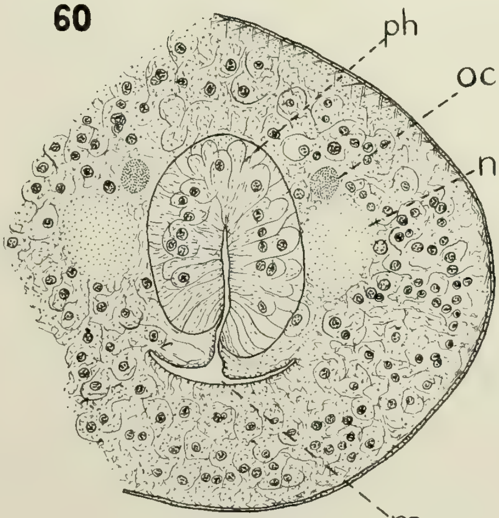

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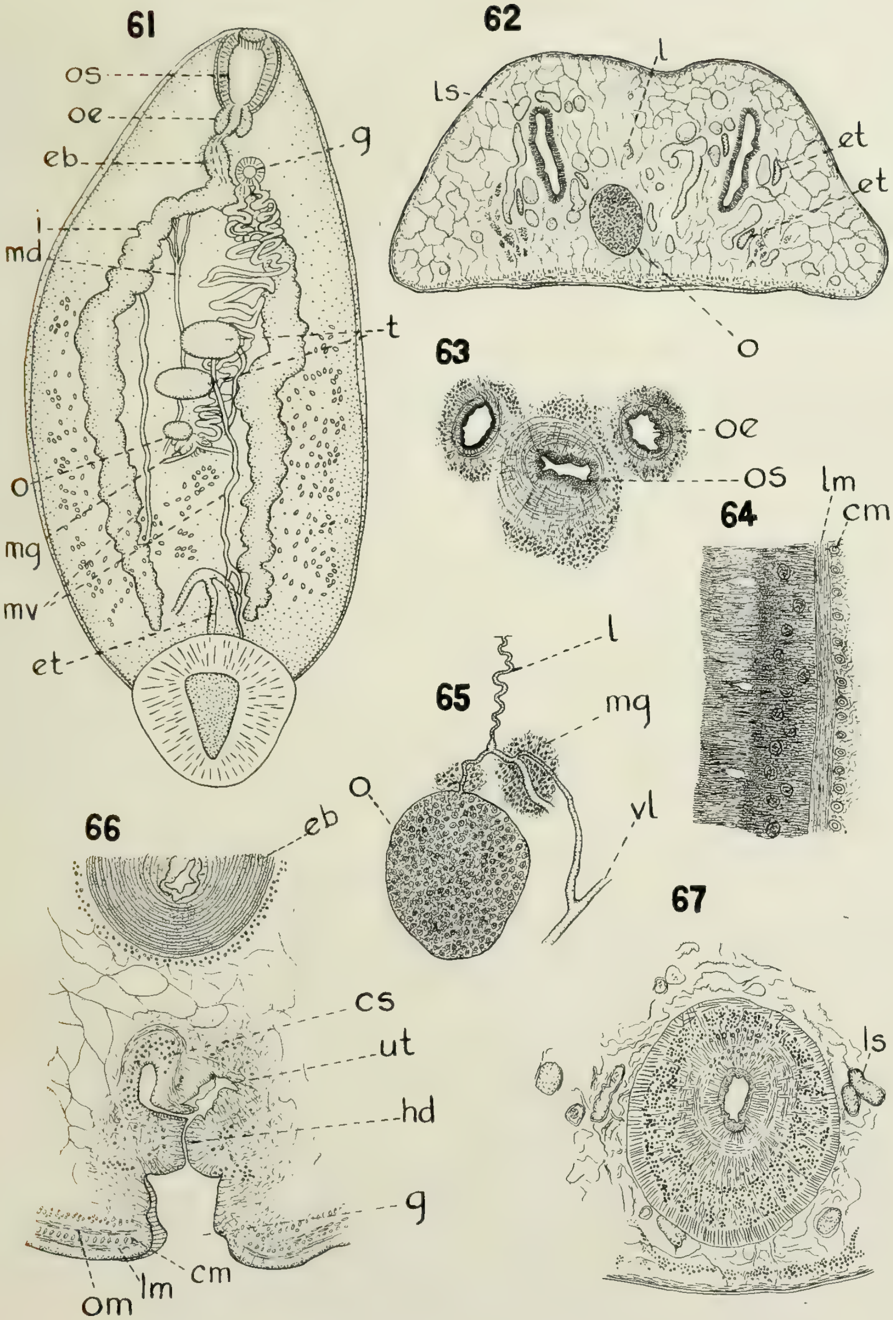
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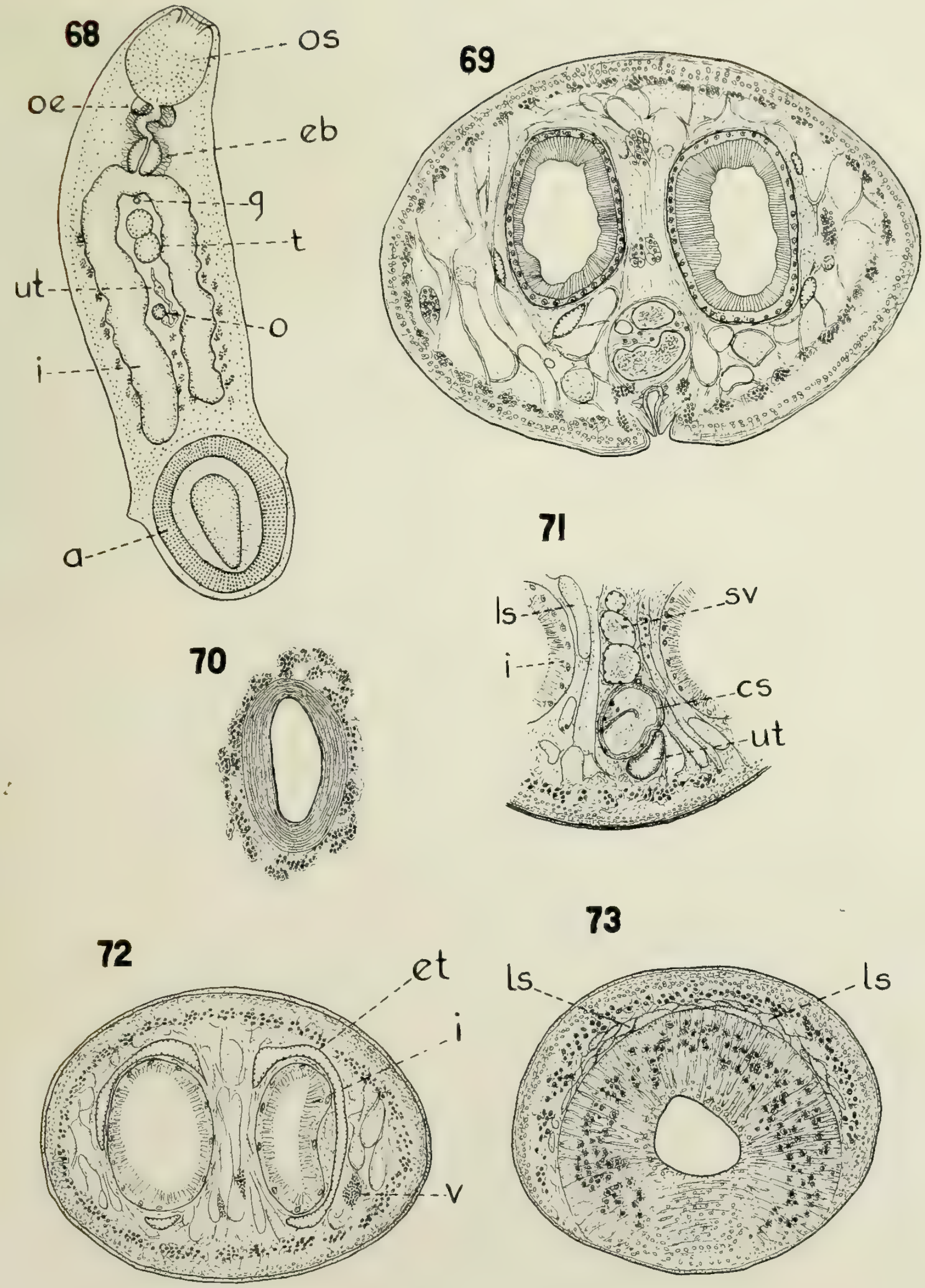
PLATE X



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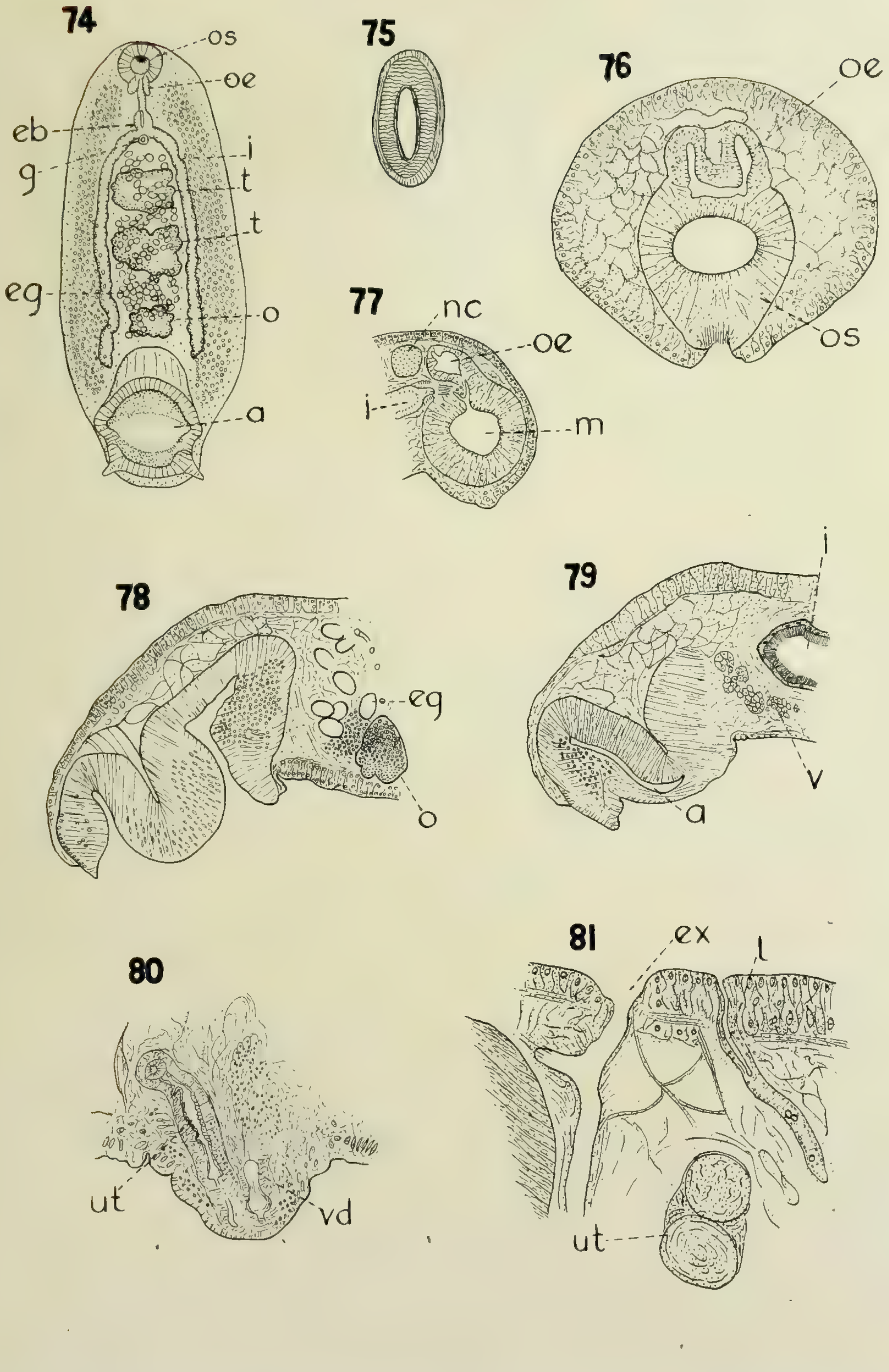
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VITA

Horace Wesley Stunkard

1889, August 23, born at Monmouth, Iowa.

1894-1901, attended public schools, Iowa.

1901-1904, attended High School, Walker, Iowa.

1904, graduated from High School.

1906-1907, attended Greenville Academy, Illinois.

1907, graduated from Greenville Academy.

1907-1908, taught in public schools, Iowa.

1908-1909, attended Greenville College, Illinois.

1909-1912, attended Coe College, Iowa.

1912, received B.S. degree, magna cum laude, Coe College.

1912-1914, Graduate Assistant in zoology, University of Illinois.

1914, (summer) Collector at Marine Biological Laboratory, Wood's Hole, Mass.

1914-1916, Fellow in zoology, University of Illinois.

1915, elected to membership in Illinois chapter of Sigma Xi.

Member: American Association for Advancement of Science, American Microscopical Society.

Publication: "Notes on the Trematode Genus Telorchis, with Descriptions of New Species".